Predicting site productivity drivers for *Podocarpus totara* and modelling its growth with 3-PG

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Abstract

Forests have been identified as key mitigation strategies to reduce net greenhouse gas emissions as they sequester and store carbon through growth. The Emissions Trading Scheme (ETS) and One Billion Tree (OBT) programme aim to increase tree plantings to offset these emissions by identifying exotic and indigenous tree species suitable for carbon sequestration across New Zealand. However, the rate of planting indigenous tree species has been slow as the species ability to sequester carbon is not well documented and legislation has prevented harvesting. The endemic conifer tōtara (*Podocarpus totara* D. Don) is an indigenous tree species which could be suitable for timber and carbon forestry. Previous studies have identified that tōtara can grow across a wide range of climatic and environmental conditions, however, few studies have investigated the key site productivity drivers and examined how they potentially influence productivity across sites. The aims of this study were to identify the main productivity drivers for tōtara across sites in the North Island of New Zealand and model growth using the 3-PG (Physiological Principles in Predicting Growth) forest growth model developed by Landsberg and Waring (1997). This study had two main hypotheses; 1) site fertility and temperature would be significant drivers of tōtara productivity and 2) the 3-PG growth model would be able to predict the growth of tōtara (stem diameter, basal area, volume, height and stand density) moderately well, providing a good fit to both the calibration and validation datasets with minimal error (RMSE).

To test these hypotheses, 21 previously described planted and naturally regenerated tōtara stands across the North Island were selected. Fifteen sites were re-measured to investigate site productivity drivers for tōtara and to calibrate the 3-PG forest growth model. A multiple linear regression analysis using the backward elimination method was conducted to examine 22 growth related variables. Reineke's (1933) stand density index (SDI) approach was used to identify trends in mortality as a function of stand density and size across sites. In addition, four volume equations by Ellis (1979), Coomes *et al.* (2002), Beets *et al.* (2012), and Todoroki and Steward (2019), that had previously been used to estimate volume of tōtara were tested to identify the most appropriate fit to two tōtara specific datasets. After model calibration, six additional sites, drawn from previous mensuration data were used to validate the model.

The results from this study identified that climatic and soil physiochemical properties were significant drivers of tōtara productivity in planted and naturally regenerated stands. Temperature (max, mean and min), rainfall, elevation, soil total phosphorus, HCP EC_a (horizontal coplanar receiver, apparent electromagnetic conductivity), and other soil macro and micronutrients (e.g. potassium and manganese) were selected as significant drivers of tōtara productivity from the multiple linear regression analysis; thus Hypothesis 1 of this study was supported. Currently, it is unclear how much these variables contribute to productivity and further research is recommended to investigate the level of contribution these significant drivers have on tōtara. Further investigation of more sites with collection of detailed growth and soil sampling data is recommended to develop a site fertility index for tōtara to quantify the role of fertility across sites. The volume equation developed by Todoroki and Steward (2019) provided the most appropriate fit to the tōtara dataset. A species-specific equation can therefore improve current estimates of volume in stands. In addition, the SDI index successfully identified relative stand densities for maximum and optimal stocking and can provide a basis for informing density management across tōtara sites.

The 3-PG forest growth model predicted the growth of tōtara across sites with variable success. The 3-PG model provided reasonable estimates of stem diameter, height and stand density across the calibration sites ($R^2 \geq 0.60$ with low RMSE). However, the model consistently over-estimated basal area and volume. The model performed poorly ($R^2 \leq 0.50$) when tested with the validation dataset, and significantly over-estimated all growth variables apart from stand density. Therefore, the results did not support Hypothesis 2. This result could be due to the limited quantity and quality of data available and further investigation into the model's parameters and algorithms is recommended. Overall, even though the results were less accurate than expected, they indicate that process-based models, like 3-PG, as opposed to empirical models, can be used to model species with limited datasets to identify base line information on growth over time and identify where additional research efforts should be directed to improve predictions.

This thesis emphasises the need to investigate a wider range of tōtara sites across varied soil fertility and productivity to improve the quality of the data available for

growth modelling and forest management. This should include regular re-measurement of growth and long-term monitoring of climatic and edaphic factors across sites. This study has significantly improved the knowledge base available for tōtara to assist landowners, forest managers, iwi and the government to grow and manage tōtara for both commercial and non-commercial purposes.

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Chapter 1

Introduction

1.1 Forestry in New Zealand

The forestry sector in New Zealand is the third largest export earner, providing approximately six billion dollars to the economy annually (Ministry for Primary Industries, 2019). Over 10 million hectares of New Zealand's total land area is covered in forestry; 8 million hectares is indigenous forestry and 2.1 million hectares is exotic plantation forests (Statistics NZ, 2005; Ministry for Primary Industries, 2019). These forests provide a range of ecosystem services, including timber, fuel, nutrient cycling and carbon storage (Pan *et al.*, 2011; Adams & Turner, 2012). With rising greenhouse gas emissions and accelerating climate change, the demand for forestry methods to reduce net greenhouse gas emissions and store carbon have increased rapidly.

The formation of the United Nations Framework Convention on Climate Change (UNFCCC) enabled countries around the world to be held accountable for their use of fossil fuels and greenhouse gas emissions (Schlamadinger & Marland, 1998; Höhne *et al.*, 2007; Ministry for the Environment, 2017). This convention provided targeted timeframes towards limiting the consumption of fossil fuels and/or increasing net carbon sequestration to limit the increase of global temperatures (Schlamadinger & Marland, 1998; Rogelj *et al.*, 2016; Ministry for the Environment, 2017). New Zealand adopted the UNFCCC in 1992, along with over 100 countries and is a signed member of the Paris agreement (2016) (Schlamadinger & Marland, 1998; Ministry for the Environment, 2017). This agreement aims to utilise land-use change and forestry to reduce or offset greenhouse gas emissions from anthropogenic activities, predominately carbon dioxide (Schlamadinger & Marland, 1998; Trotter *et al.*, 2005; Palmer *et al.*, 2010). Forests can store and sequester large amounts of carbon dioxide (CO_2) from the atmosphere via photosynthesis (Allen *et al.*, 2013). Globally, forests contain approximately 77% of all terrestrial above ground carbon, therefore, planting and maintaining forests have been recognised as options to help offset greenhouse gas emissions (Schlamadinger & Marland, 1998; Ashton *et al.*, 2012).

Carbon sequestration can occur at different rates depending on the type of species present and the type of forest (e.g. mixed indigenous forests, or homogeneous plantation forests) (Whitehead *et al.*, 2001; Trotter *et al.*, 2005; Allen *et al.*, 2013). When plantation forests are harvested or as trees decay, carbon is released back into the atmosphere. Plantation forests are forests which are planted, managed and harvested to produce wood for commercial purposes (Carnus *et al.*, 2006; Sedjo, 2015). These forests can be comprised of exotic or indigenous species (Carnus *et al.*, 2006). Given the longevity of indigenous tree species opposed to exotic trees, planting more indigenous species could create an additional carbon sink to help offset or reduce the loss of storage from plantation forests (Trotter *et al.*, 2005). There is a growing amount of interest in how to manage these systems and what species to plant to optimise carbon sequestration and storage (Trotter *et al.*, 2005; Palmer *et al.*, 2010; Höck *et al.*, 2017). Indigenous tree species have the potential to be utilised as carbon forests to help offset greenhouse gas emissions while providing opportunities for commercial, cultural and environmental benefits (Allen *et al.*, 2013; Höck *et al.*, 2017). However, compared to common plantation species, there is a lack of information regarding growth, yield and silvicultural management for indigenous tree species which has slowed progress towards the adoption of indigenous afforestation in forestry (Allen *et al.*, 2013; Höck *et al.*, 2017).

In the early 1900s, New Zealand's indigenous forests were depleting at a rapid rate (Hinds & Reid, 1957; Cameron, 1962; Brockerhoff *et al.*, 2008; Allen *et al.*, 2013). These forests were intensely harvested for timber or felled to clear land for agriculture and other land uses (Hinds & Reid, 1957; Cameron, 1962; Brockerhoff *et al.*, 2008; Allen *et al.*, 2013). Three genera or families dominated the timber being extracted from these indigenous forests: *Nothofagaceae* (e.g. Silver beech *Nothofagus menziesii* (Hook.f) Oerst.), *Araucariaceae* (Kāuri *Agathis australis* (D. Don) Lindl.), and *Podocarpaceae* (e.g. Rimu *Dacrydium cupressinum* Lamb.) (Allen *et al.*, 2013; Simpson, 2017). The growing demands for timber and wood supplies within New Zealand started to surpass the indigenous wood supply, leading to the introduction of fast growing species in order to cope with the high demand for timber (Hinds & Reid, 1957; Cameron, 1962; Brockerhoff *et al.*, 2008). Exotic species such as radiata pine (*Pinus radiata* D. Don), Douglas-fir (*Pseudotsuga menziesiii* (Mirb.) Franco), eucalypts (e.g. *Eucalyptus fastigata* H. Deane & Maiden), and other species were introduced to a proportion of the areas

(approx. 7% of NZs total land area) which were previously covered by indigenous forests (Hinds & Reid, 1957; Cameron, 1962; Brockerhoff *et al.*, 2008; Ministry for Primary Industries, 2019). Currently, exotic plantation forests cover approximately 1.75 million ha of New Zealand's total land area, with radiata pine accounting for 90% of these forests (Palmer *et al.*, 2010; Ministry for Primary Industries, 2019). Approximately 80% of the remaining indigenous forests are owned by the crown and are managed by the Department of Conservation for conservation and recreation (Bergin, 2001; Allen *et al.*, 2013). The remaining 20% of the indigenous forests (1.5 million ha) are owned by private landowners including iwi and other māori organisations (Brockerhoff *et al.*, 2008; Allen *et al.*, 2013). These forests are a mixture of the original indigenous vegetation and vegetation that has regenerated following changes in land use (Bergin, 2001; Brockerhoff *et al.*, 2008). To prevent forests from further degradation, frameworks and policies were created to govern how forests are used (Allen *et al.*, 2013). The New Zealand Government introduced the Resource Management Act 1991 and the Forests Act 1949 to ensure the sustainable supply of timber from indigenous and plantation forests (Walker *et al.*, 2006; Brockerhoff *et al.*, 2008; Allen *et al.*, 2013; Cieraad *et al.*, 2015). New Zealand's commitment to the UNFCCC and Kyoto Protocol led to the introduction of the Emissions Trading Scheme (ETS) and the creation of the One Billion Tree (OBT) Programme (Trotter *et al.*, 2005).

The ETS was introduced by the New Zealand Government in 2008, in an attempt to help mitigate greenhouse gas emissions and meet its international obligations to reduce carbon emissions (Jiang *et al.*, 2009; Adams & Turner, 2012; Ministry for Primary Industries, 2017, 2019). The scheme enables emitting and sequestering parties to trade emission units (or carbon credits) to account for their own emissions and provide financial incentives to reduce them (Ministry for Primary Industries, 2017; Ministry for the Environment, 2019). Emitting parties like agricultural, industrial and waste industries must purchase carbon credits to balance their emissions, whereas sequestering parties such as those involved in the forestry industry are able to sell their credits based on the amount of carbon their forests sequester (Jiang *et al.*, 2009; Ministry for Primary Industries, 2017; Ministry for the Environment, 2019). An important aspect of this scheme is estimating how much carbon different forest types can store (Allen *et al.*, 2013). To simplify this for landowners and forest managers, the Ministry for Primary Industries (2017)

developed carbon look-up tables with pre-calculated estimates of carbon sequestration (tonnes of carbon dioxide (CO_2) equivalents per hectare) by age and forest type. Both radiata pine and Douglas-fir have species-specific carbon look-up tables as growth rates and growth models for both species under New Zealand conditions are available. However, the carbon look-up tables for indigenous forest species are generalised and cannot account for the wide range of forest species and silvicultural regimes. Thus, it highlights the need for accurate forest growth models which can be used to estimate carbon and to plan future plantings for specific forest types (Vanclay & Skovsgaard, 1997; Vanclay, 2003; Ministry for Primary Industries, 2017).

More recently, the OBT Programme was created by the New Zealand Government with support from Te Uru Rākau and the Ministry for Primary Industries (Ministry for Primary Industries, 2019; Ministry for the Environment, 2019). This programme aims to increase the current rates of afforestation, setting the goal of planting one billion trees within the next decade to help offset greenhouse gas emissions (Ministry for the Environment, 2019). Funding from the programme provides an incentive to landowners to plant on their land to increase sequestration and help reduce erosion and nutrient runoff, using both exotic and indigenous species (Ministry for Primary Industries, 2018; Ministry for the Environment, 2019). Research over the last thirty years has focused on identifying the growth and yield of common plantation species that might be suitable for offsetting emissions (Battaglia & Sands, 1998). Indigenous forest species such as kāuri, rimu and tōtara are some just some of the alternative forest species which are now generating increased interest from landowners due to the commercial, cultural and environmental benefits (Bergin, 2000, 2003b; Bergin & Kimberley, 2003; Simpson, 2017). However, the forestry literature lacks sufficient quantitative information on the growth, yield, ecological preference and various other aspects of these alternative forest species (Allen *et al.*, 2013). This highlights the need for further species-specific information to help inform planting and management decisions.

1.2 Tōtara

Lowland tōtara (*Podocarpus totara* D. Don) hereafter referred to as tōtara, is one of New Zealand's treasured endemic conifers (Hinds & Reid, 1957; Bergin, 2001; Simpson, 2017). Tōtara is highly valued commercially, culturally and ecologically

by Māori and Europeans (Hinds & Reid, 1957; Wilson & Owens, 1999; Bergin, 2000; Ministry for Primary Industries, 2019). In New Zealand, tōtara is one of four closely related species (Hinds & Reid, 1957; Bergin, 2001; Simpson, 2017). The three close relatives are Hall's tōtara (*Podocarpus laetus* Hooibr. ex Endl.), needle-leaved tōtara (*Podocarpus acutifolius* Kirk) and snow tōtara (*Podocarpus nivalis* Hook.) (Hinds & Reid, 1957; Bergin, 2000; Kirk, 1889, cited in Simpson, 2017). New Zealand *Podocarpus* species can hybridise easily to form various intermediate forms or new varieties such as Westland tōtara (*Podocarpus totara* var. *waihoensis* Wardle) (Wardle, 1972; Bergin, 2000; Simpson, 2017). Compared to the other species, tōtara and Halls tōtara are more widespread and are particularly difficult to differentiate as their morphologies are similar (Gardner, 1990; Simpson, 2017). The ecological preferences differ between the two as Hall's tōtara is generally found at higher altitudes and less fertile sites compared to tōtara which is found at lower altitudes and more fertile sites (Gardner, 1990; Matsui *et al.*, 2004; Simpson, 2017).

Tōtara is a long-lived species which is relatively tolerant of a wide variety of environmental conditions, such as frost, wind and drought (Hinds & Reid, 1957; Bergin, 2000, 2001; Simpson, 2017). Mature tōtara can reach heights greater than 30 metres, with stem diameters more than 2 m in size (Figure 1.1) (Hinds & Reid, 1957; Bergin, 2001; Simpson, 2017). The species is not tolerant of full shade conditions, therefore it is often found occupying sunny open sites or establishing in tree fall gaps in mixed podocarp forests amongst other native conifers such as kāuri, rimu, miro (*Prumnopitys ferruginea* (G. Benn. ex D. Don) de Laub.), and mataī (*Prumnopitys taxifolia* (D. Don) de Laub.) (Bergin, 2000, 2001; Bergin & Kimberley, 2003; Simpson, 2017). The species is distributed throughout New Zealand in indigenous lowland and montane forests from sea level up to 600 m (Hinds & Reid, 1957; Bergin, 2000; Bergin *et al.*, 2008; Simpson, 2017). The species is most abundant in northern regions, down to the central North Island and is found intermittently in the South Island and on Stewart Island (Hinds & Reid, 1957; Bergin & Kimberley, 2003). In Northland, the regeneration rate of the species is high enough for it to be considered a weed by some landowners (Bergin, 2000). The high quality of tōtara timber and its rapid depletion over the years due to the overharvesting of old-growth tōtara has increased the demand for research regarding the species and its ecological preferences. Hinds and Reid (1957), Simpson (2017), and Bergin (2001) largely dominate the literature with their

detailed descriptions of tōtara trees, their ecology, and the cultural value of the species in New Zealand.

Figure 1.1. Tōtara trees in a regenerated stand in Northland.

The leaves of tōtara are narrow, linear, and pointed sharply at the apex (Figure 1.2) (Hinds & Reid, 1957). Leaves are predominately green, however, can often appear slightly pigmented by brown, yellow, and purple hues (Hinds & Reid, 1957; Simpson, 2017). Juvenile tōtara have long, thin leaves which are arranged on the stem in a spiral pattern (Hinds & Reid, 1957; Philipson & Molloy, 1990; Bergin, 2000; Simpson, 2017). On mature trees, leaves are short, thick and leathery, and are arranged in two opposite rows on the stem (Figure 1.2) (Hinds & Reid, 1957; Philipson & Molloy, 1990; Bergin, 2000; Simpson, 2017). The roots of mature tōtara trees are shallow and nodular, their spread usually extends beyond the spread of the crown (Hinds & Reid, 1957; Bergin, 2000; Simpson, 2017). The root system is highly variable and irregular as individuals growing in the same environment exhibit different root structures (Bergin, 2000; Simpson, 2017).

Figure 1.2. Leaves on a mature tōtara tree.

A key characteristic of the species is its bark (Hinds & Reid, 1957; Bergin, 2000; Simpson, 2017). Tōtara trees have thick, fibrous, stringy bark which has a distinctive orange-brown or reddish-brown colour (Hinds & Reid, 1957; Bergin, 2000; Simpson, 2017). The form of the stem can vary depending on the topography and density of the stand (e.g. steepness of slope and stocking rate) (Bergin, 2000; Simpson, 2017). Individual trees will generally grow quite large and broad in areas with little competition, which is often why tōtara are seen in the landscape with large green crowns and multiple leaders (Bergin, 2000; Cown *et al.*, 2009; Simpson, 2017). The trunks of mature tōtara are buttressed at the base, while the stems are relatively straight until the main leader declines and the surrounding branches grow outwards (Bergin, 2000; Simpson, 2017). In stands were the stocking is high, trees generally have a relatively good stem form for timber production (e.g. single leaders with minimal number of small knots) (Bergin & Kimberley, 2003; Cown *et al.*, 2009; Simpson, 2017). Due to the long life of individual trees, old tōtara are generally hollow (Simpson, 2017). Identifying the correct age of trees can be difficult, however, studies have found that tōtara are able to grow to approximately 1000 years old, and they reach old age at approximately 500 years (Bergin, 2000; Simpson, 2017). The largest known living tōtara tree in New Zealand is Pouakani (40 m in height, with a diameter of 3.8 m) which is estimated to be approximately 1000 years old (Simpson, 2017). The tree is found near Pureora forest in the south Waikato, in an isolated forest fragment which is presently surrounded agriculture, but was once part of the larger Pureora forest (Bergin, 2000; Graham *et al.*, 2012; Simpson, 2017).

Compared to other native species the seedling survival rates of tōtara in nurseries are relatively high (Beveridge, 1962; Bergin, 2003b). The relative ease of germination and high survivability of seedlings is why tōtara are considered one of the easiest native trees to grow (Beveridge, 1962; Bergin, 2003b, 2003a). Seedlings are often planted under a nursery crop of mānuka (*Leptospermum scoparium* J. R. Forst) or kānuka (*Kunzea ericoides* (A. Rich) Joy Thomps.) to enhance survival and reduce frost damage (Beveridge, 1962; Bergin, 2000). The species is tolerant of a wide range of conditions, but is light demanding (Bergin, 2000). Competition from weeds and other species can hinder the growth of tōtara seedlings, therefore it is recommended that weed management is incorporated into management plans to increase survival rates (Beveridge, 1962; Bergin, 2000).

Tōtara is dioecious, with separate male and female trees (Simpson, 2017). The reproductive cycle occurs over an 18-month period from the initiation of the male cone, through to the formation of the mature seed (McEwen, 1988; Wilson & Owens, 1999; Bergin, 2000; Simpson, 2017). Female cones become receptive in spring, along with the release of pollen from the male cones (Hinds & Reid, 1957; Bergin, 2000; Simpson, 2017). The success of reproduction is largely due to the vast amount of wind-borne pollen and the delayed development of the female cone (Bergin, 2000). After fertilisation and further development of the female cone, seeds with red fleshy receptacles are present from March to April (Bergin, 2000). These seeds can be found at the base of female trees, and are distributed by native and exotic bird populations such as kaka (*Nestor meridionalis* Gmelin), tūī (*Prosthemadera novaeseelandiae* Gmelin), kererū (*Hemiphaga novaeseelandiae* Gmelin) and yellow-crowned parakeets (*Cyanoramphus auriceps* Kuhl) (Bergin, 2000; Simpson, 2017). As the trees produce seeds annually, pests and diseases can impact the success of seeding (Bergin, 2000; Simpson, 2017).

1.2.1 Pests / diseases

Insect browsing, pathogens, and other harmful agencies can severely damage the growth and longevity of tōtara that have not surpassed their seedling stage (Beveridge, 1962; Bergin, 2000). A study by Beveridge (1962) analysed the growth of native podocarp seedlings in Pureora Forest Nursery. Frost damage was found to hinder seedling growth, particularly the height of the seedlings when frosts occur at

unseasonable times (Beveridge, 1962; Bergin, 2000). Insects such as defoliating caterpillars (*Ctenopseustis obliquana* Walker and *Pseudocoremia suavis* Butler), longhorn beetles (*Coptomma lineatum* F. and *Ambeodontus tristis* F.), and cicadas (*Amphipsalta zealandica* Boisduval and *Amphipsalta cingulata* F.) can cause irreversible damage to young individuals, altering their growth and structure (Beveridge, 1962; Bergin, 2000, 2003a). New growth is often favoured by the insects, therefore young seedlings are highly susceptible to severe defoliation, compared to saplings and mature trees which are able to recover faster from the damage (Beveridge, 1962). Severe damage can hinder and alter growth of the individual, resulting in stunted trees or individuals with multiple leaders. With appropriate insecticide treatment, the severity of the attacks can be reduced (Beveridge, 1962). Canopy die-back is common in indigenous species when they are defoliated by browsing animals or infected by pathogens (Simpson, 2017). Young tōtara are particularly susceptible to infection from *Corynelia tropica*, a fungus which forms spots on leaves and can disfigure new foliage (Hood, 1985; Simpson, 2017). The fungus is harmless to the survival and longevity of mature trees; however, depending on the severity of the infection it can affect shoot growth and destroy fruits (Simpson, 2017).

Tōtara can be damaged by browsing animals in the forest (Bergin, 2003b). Red deer (*Cervus elaphus scoticus* L.), and possums (*Trichosurus vulpecula* Kerr) were found to cause damage to the species in studies by Rogers (1997) and Nugent *et al.* (1997). The authors identified possums as the most significant threat to the species, as they feed on juvenile and mature tōtara, defoliating branches and most of the canopy (Bergin, 2000). Possum feed on the fleshy seeds, therefore a small population could cause significant damage to tōtara stands, and their ability to reproduce (Nugent *et al.*, 1997; Ebbett, 1998; Bergin, 2000). Grazing pressure from stock can also alter the dynamics of regenerated and natural tōtara (Simpson, 2017). Trampling can reduce regeneration of the species where stock presence is high (Bergin, 2000, 2003b). The exposed roots and stems of tōtara can be damaged by livestock stripping the bark or trampling the roots (Bergin, 2003b; Simpson, 2017). This can cause infection or issues with water uptake (Simpson, 2017). Furthermore, substantial damage to individual trees or stands could lead to decreased wood quality and lower economic returns for landowners (Bergin, 2000; Simpson, 2017).

1.2.2 Commercial value

Commercially, tōtara is regarded as a specialty timber due to its high-quality wood (Hinds & Reid, 1957; Bergin, 2003b). The timber's durability and ease of working led to its widespread use by both Māori and European settlers (Hinds & Reid, 1957; Bergin *et al.*, 2008; Cown *et al.*, 2009). The wood resources from the species were predominantly used for building, fencing, joinery, carving and canoe construction (Bergin, 2000; Bergin *et al.*, 2008; Phillips, 2017; Simpson, 2017). The wood is resistant to the common furniture borer (*Anobium punctatum* De Geer) which prevented damage even while awaiting milling (Phillips, 2017; Simpson, 2017). Tōtara as a timber resource became depleted as rapid exploitation exceeded the ability of the tōtara stands to replenish (Bergin & Kimberley, 2012). Primarily the tōtara harvested and milled for timber by early settlers were large old growth trees, while both young and mature tōtara were mainly lost due to land-use change (Bergin & Kimberley, 2012). The demand for wood often exceeded supply, which increased the value of the timber resource (Allen *et al.*, 2013). Later, government restrictions placed on harvesting indigenous forest species from natural forests and private land ensured the sustainability of the timber resource (Bergin, 2000; Cown *et al.*, 2009; Allen *et al.*, 2013). As tōtara has not been harvested commercially for many years, the value of the timber is difficult to quantify (Steward *et al.*, 2018; Quinlan, 2019). However, recent harvest trials in Northland have identified the commercial value is estimated to be between $135 – $150 per cubic metre at stumpage (Quinlan, 2019).

The Northland Tōtara Working Group (NTWG) and Tane's Tree Trust (non-profitable charitable trust) are key parties working towards utilising tōtara for timber and carbon forestry in the northern regions of the North Island where the species grows prolifically (Figure 1.3) (Bergin, 2000; Quinlan *et al.*, 2011; Steward *et al.*, 2018). The production of high quality wood from regenerated and planted tōtara stands, and afforestation of new sites could potentially provide jobs and economic opportunities to this region, adding further value to the species (Bergin, 2000; Bergin & Kimberley, 2003). Indigenous forests can provide multiple services including commercial and non-commercial benefits (Allen *et al.*, 2013). Areas forested with tōtara can be utilised for recreation, tourism, heritage, research, conservation and biodiversity (Bergin, 2000; Allen *et al.*, 2013; Simpson, 2017).

Figure 1.3. Naturally regenerated tōtara trees growing in cohorts in Northland.

1.3 Significance of this research

This research aims to provide more confidence to landowners, iwi, forestry managers and the government when predicting growth of tōtara around New Zealand. The results from this study will aim to fill the knowledge gaps regarding how the growth of tōtara varies in response to different soil and climate conditions, and what environments are suitable for the optimal growth of the species. This research will provide information for landowners and iwi about whether their land is suitable for timber or carbon forestry. The commercial, cultural, ecological and economic benefits from growing tōtara in forest stands could see the demand and utilisation of the species increase (Bergin, 2000). The cultural significance of the species could also lead to further planning of afforestation, particularly on Māori land where the species could be planted and managed for carbon forestry or harvested sustainably for timber (Bergin, 2000; Quinlan, 2011; Quinlan *et al.*, 2011). Concurrently, afforestation with tōtara will help New Zealand fulfil its goals within the OBT Programme.

1.3.1 Knowledge Gaps

The knowledge base for indigenous forest species in New Zealand has grown over the years, however, there are still substantial gaps compared to common forest

species such as pine and eucalypts (Coops *et al.*, 1998; Meason *et al.*, 2011; Höck *et al.*, 2017). The slow growth and longevity of the species has discouraged research (Hinds & Reid, 1957; Bergin, 2000; Simpson, 2017). Compared to fast growing plantation species, which enables faster returns on investments (e.g. approximately 20-30 years) and more than one rotation (crop) over the length of time to grow one rotation of a slower tree species, the commercial and economic benefits of planting or managing tōtara may require decades before they are realised (e.g. approximately 80 – 100 years) (Hinds & Reid, 1957; Bergin, 2000; Simpson, 2017). The ETS and OBT Programme have increased the demand for further research on indigenous forest species (Bergin, 2000; Allen *et al.*, 2013). Collaboratively, Scion and the Ministry for Primary Industries (MPI) have been working on Sustainable Land Management and Climate Change (SLMACC) projects. One of these is the Growing Diversity project which is investigating the potential of less common planted exotic and indigenous species which have the potential to be suitable for offsetting greenhouse gas emissions (Höck *et al.*, 2017; Lin *et al.*, 2018). Tōtara is one of these species, therefore further research will help improve the accuracy of growth and yield models and provide substantial improvements to the current knowledge base of tōtara to help with future management decisions regarding the use of the species for timber and carbon forestry (Bergin, 2000; Bergin & Kimberley, 2003; Höck *et al.*, 2017; Simpson, 2017; Lin *et al.*, 2018).

The ETS currently separates the carbon look up tables based on the dominant tree species, categorising Radiata pine, Douglas-fir, exotic hardwoods, exotic softwoods and indigenous forests as the main forest species. These tables enable land use managers and owners to estimate how many tonnes of carbon dioxide equivalents per hectare their forests sequester at a specified stand age. The information available for the common plantation species of radiata pine and Douglas-fir are more detailed than that of indigenous forests, as the look up tables for these species are available for a range of ages and regions around New Zealand. As the use of indigenous forests becomes more favourable to landowners and forest managers, there is growing potential that the carbon look-up tables will be revised to provide more accurate estimates for indigenous forest types. A key aspect of this would be the need for further studies on these species to ensure the tables provide reliable predictions for forest managers, landowners and the government. Growth and yield models can be utilised to obtain this data from indigenous forest species, as they

can be parameterised to specific species across a range of forest sites (Battaglia & Sands, 1998; Whitehead *et al.*, 2001).

1.3.2 Growth and yield models

The demand to accurately predict tree growth in response to changing environmental conditions has led to the development of forest growth models (Kirschbaum, 1999; Johnsen *et al.*, 2001; Landsberg & Sands, 2011; Weiskittel *et al.*, 2011). Mathematical models are used in forestry to understand forest dynamics over time, by estimating current growth and forecasting future yields (Peng, 2000; Landsberg & Sands, 2011; Weiskittel *et al.*, 2011). Husch *et al.* (2002) and Weiskittel *et al.* (2011) defined growth as changes in tree volume, weight and form from one period of time to the next. Yield can be defined as the amount of timber produced by an individual and/or stand (Amaro *et al.*, 2003; Steward, 2011). Since the early 1850s, forestry mensuration data has been the primary source of growth and yield modelling (Peng, 2000; Steward, 2011). The data were predominately used to predict the growth of the forest stand and timber yield before harvest (Peng, 2000). A wide array of forest growth models have been developed and altered since the 1930s to successfully fit the desired goal of users; whether the growth models are required for research or management purposes (Xenakis *et al.*, 2008; Weiskittel *et al.*, 2011). Models were commonly utilised by forest managers to predict timber production yields and provide a basis for silvicultural management to increase economic returns (Rodríguez-Suárez *et al.*, 2010).

Forest growth models vary in their ability to simulate tree growth, with advantages and disadvantages to each one (Weiskittel *et al.*, 2011). A key aspect of growth and yield modelling are the models' abilities to accurately predict growth at different spatial and temporal resolutions (Weiskittel *et al.*, 2011). Spatial resolution refers to the scale of the model, whether the model operates at a small resolution such as on an individual leaf or tree basis, or at a larger resolution, encompassing whole stands or forests (Steward, 2011; Weiskittel *et al.*, 2011). The temporal resolution of models can differ from hourly time steps, through daily, monthly, yearly and even decade time scales depending on what specificity the researcher requires (Weiskittel *et al.*, 2011). These resolutions are dependent on the type of data

available and the complexity of the model (Xenakis *et al.*, 2008; Weiskittel *et al.*, 2011).

There are three main categories of growth models that differ in robustness and complexity: empirical, process-based, and hybrid models (Landsberg & Sands, 2011). Empirical models were developed to predict growth and yield over time for forest stands from inputs of statistical data (Johnsen *et al.*, 2001; Landsberg & Sands, 2011; Weiskittel *et al.*, 2011). These simplistic models are able to consolidate large amounts of data, which can be from species of various stands, sites and ages to predict future growth based on previous growth measurements (Goulding, 1994; Johnsen *et al.*, 2001; Pinjuv *et al.*, 2006; Landsberg & Sands, 2011). These models were not designed to understand the underlying mechanisms influencing growth, but to help inform forest management decisions to improve economic returns (e.g. thinning and harvesting) (Pinjuv *et al.*, 2006; Landsberg & Sands, 2011). Limitations to these models are in their abilities to forecast growth and yield for conditions which are not the same as those they were derived from, as the models assume the individual tree or stand will continue to grow under the same conditions (Pinjuv *et al.*, 2006; Landsberg & Sands, 2011; Weiskittel *et al.*, 2011). Empirical models can be used to examine differences in growth by analysing trends (linear and non-linear) over time (Weiskittel *et al.*, 2011). Regional stand level models were developed to predict the performance of radiata pine in New Zealand (García, 1999). Models such as KGM3 (central North Island), CLAYS (Auckland) and CANTY (Canterbury) were used in conjunction with computer modelling systems (e.g. STANDPAK) to predict growth across different regions e.g. central North Island versus Southland (García, 1999). The division of data into separate regional models enabled predictions which were more accurate and provided comparisons of growth between the regions (García, 1999).

The site index concept is a key feature commonly used in conjunction with empirical growth models. Site index refers to the timber potential of a site dominated by a single species, at a base reference age (Burkhart & Tennent, 1977; Battaglia & Sands, 1998; Waterworth *et al.*, 2007; Steward, 2011; van der Colff & Kimberley, 2013). The base reference age is generally near the end of the rotation for a species, therefore for radiata pine plantations in New Zealand, the reference age is approximately 20 years after planting (Burkhart & Tennent, 1977; Watt *et*

al., 2010; van der Colff & Kimberley, 2013). The mean top heights of trees within the stand (mean height of the 100 largest stem diameters per hectare) are commonly used for site index as the primary value to predict growth, as site quality is often reflected by height growth (e.g. poor site quality should exhibit reduced height growth compared to good site quality) (Burkhart & Tennent, 1977; Battaglia & Sands, 1998; Steward, 2011; van der Colff & Kimberley, 2013). Most height vs age functions require a measure of site index (van der Colff & Kimberley, 2013). Other methods of measurement can be incorporated into the site index to improve the robustness of the concept (Battaglia & Sands, 1998; Steward, 2011). For example, in New Zealand the 300 index can also be used to estimate productivity for radiata pine (Kimberley *et al.*, 2005; Watt *et al.*, 2010). The 300 index is a measure of stem volume mean annual increment (MAI) at 30 years after planting with a silvicultural regime of 300 stems ha^{-1} (Watt *et al.*, 2010). The estimates of productivity for radiata pine are calculated using an empirical stand level model called the 300 index (Kimberley *et al.*, 2005; Watt *et al.*, 2010). Compared to site index, the 300 index is superior as it incorporates age and stocking compared to just age (Kimberley *et al.*, 2005; Watt *et al.*, 2010). However, both approaches are limited in their ability to predict growth when site conditions do not remain constant (Burkhart & Tennent, 1977; Goulding, 1994; Battaglia & Sands, 1998; Johnsen *et al.*, 2001; Waterworth *et al.*, 2007; Steward, 2011).

In recent years, models have shifted from highly statistical empirical models, towards more mechanistic models as they focus on the key processes which influence the growth and productivity of forests, such as light interception, fertility and carbon allocation (Pinjuv *et al.*, 2006; Landsberg & Sands, 2011; Weiskittel *et al.*, 2011). The development of these models has followed technological advancements and knowledge of tree ecophysiology (Goulding, 1994; Johnsen *et al.*, 2001). Process-based modelling is a multifaceted approach which includes the physiology and ecology of the species and its environment to predict growth and yield (Johnsen *et al.*, 2001; Pinjuv *et al.*, 2006). The complexity of the model enables users to predict growth and forecast yields of certain species from little data, and extend the predicted range of growth further than empirical models, while maintaining accuracy (Goulding, 1994; Pinjuv *et al.*, 2006; Landsberg & Sands, 2011). A key use of these forestry growth models are to estimate future states of forest growth across abiotic and biotic gradients for sustainable forest management

(Peng, 2000; Hasenauer, 2006). These models can be used to identify potential sites for afforestation as they can account for future climate and soil differences to recommend suitable forest management for the species (Goulding, 1994; Rodríguez-Suárez *et al.*, 2010).

The use of process-based models was initially slow with the models used mainly for research rather than practical forestry tools. However, closely related process-based models now dominate the literature, for example JABOWA, MAESTRO, BIOMASS, CABALA, BIOME-BGC and 3-PG (Coops *et al.*, 1998; Mäkelä *et al.*, 2000; White *et al.*, 2000; Johnsen *et al.*, 2001). Each of these models differ in their ability to accurately predict growth at different spatial and temporal resolutions (Battaglia & Sands, 1998). These models can also be used in mixed stands, and uneven aged stands depending on the model's capabilities (Mäkelä *et al.*, 2000). Most of these models have not been tested on many species other than conifers and deciduous forest types (Battaglia & Sands, 1998; Coops *et al.*, 1998). A limitation of process-based models is the complexity of their design which makes it difficult for landowners and some forest managers to utilise, as they often require specific physiological values which are difficult to obtain (Mäkelä *et al.*, 2000; Pinjuv *et al.*, 2006). An understanding of the theory and processes behind the models is key to understanding how management should be planned based on model outputs, and whether the predictions are reasonable for the target species (Hasenauer, 2006). The successful development of process-based models has enabled further improvements to the information available on alternative forest species and their management (Battaglia & Sands, 1998). Utilisation of these models on species with limited data resources could enable forest managers and landowners to prepare forests for the changing conditions and manage them accordingly to ensure their future health and sustainability under climate change (Meason & Mason, 2014).

In addition to process-based models, hybrid growth models can be relevant for forest management (Battaglia & Sands, 1998). Hybrid models incorporate simplified features of empirical and process-based models, this includes using inputs from empirical growth data in addition to climate and site variables to predict growth (Monserud, 2003). However, further research is needed to understand how well these models work at different spatial and temporal resolutions (Battaglia & Sands, 1998). Most of these models incorporate additional analysis tools such as

the use of Geographic Information Systems (GIS) or remote sensing technology (e.g. TRIPLEX) (Peng *et al.*, 2002; Zhang *et al.*, 2008; Coops & Waring, 2011; Meason *et al.*, 2011; Meason & Mason, 2014). Often studies combine empirical and process-based models to create hybrid models which are able to provide more robust and expeditious analyses for forest managers (e.g. PROMOD and NITGRO and Forecast Climate (Battaglia *et al.*, 1999; Seely *et al.*, 2015). The decision as to which type of model to use is largely dependent on the type of data available and the objectives of the research. It is important to remember that all forest models have aspects which are not necessarily applicable to certain forest stands or species, therefore model selection should be site, species and goal orientated to provide the most appropriate outputs for researchers and forest managers (Battaglia & Sands, 1998; Mäkelä *et al.*, 2000).

1.3.3 3-PG Forest Growth Model

The 3-PG forest growth model (physiological processes for predicting growth) is a generalised process-based model which has shown promising results for modelling growth of a variety of fast growing monoculture species (e.g. pine and eucalypts) around the world (e.g. North and South America, South Africa, Australia and Western Europe) (Mäkelä *et al.*, 2000; Amichev *et al.*, 2010; Feikema *et al.*, 2010; Rodríguez-Suárez *et al.*, 2010). The stand-level model first developed by Landsberg and Waring (1997) requires a combination of abiotic and biotic variables as inputs to simulate observed growth and forecast future changes to tree biomass and productivity (Landsberg & Waring, 1997; Nightingale *et al.*, 2008; Feikema *et al.*, 2010). A key feature of process-based models is their ability to utilise small datasets to predict growth of the target species for regions outside of the species current distribution (Landsberg & Waring, 1997; Landsberg *et al.*, 2003). The 3-PG model bridges the gap between traditional empirical based models and process based models by its simplicity (Sands & Landsberg, 2002). As the model is neither site nor species specific, it can be used on any species once it is parameterised for that species (Sands & Landsberg, 2002). This growth model can be used by researchers to identify afforestation sites which are suitable for timber or carbon forestry (Landsberg & Waring, 1997; Coops *et al.*, 1998).

The 3-PG model operates on a monthly temporal resolution, requiring monthly climate data for rainfall, temperature, solar radiation and frost days (Landsberg & Waring, 1997). As long as climate data is available, the model can run for a number of years which means it can be used to predict growth of older species (Landsberg & Waring, 1997; Coops *et al.*, 1998; Landsberg *et al.*, 2003). Two sets of calculations form the basis of the model; calculations that contribute to biomass formation and calculations that allocate the biomass to different components of the tree and simulate growth (Landsberg *et al.*, 2003). The model is used to calculate the growth of known species in forest stands (Coops *et al.*, 1998). At a stand level the model can output stem mass, volume, growth rate, carbon allocation and leaf area of the target species which are highly relevant to forest managers (Landsberg & Waring, 1997; Coops *et al.*, 1998; Landsberg *et al.*, 2003; Rodríguez-Suárez *et al.*, 2010).

The utilisation of 3-PG around the world is facilitated by the combination of empirical data and physiological data which simplifies the growth modelling process (Landsberg & Waring, 1997). Rodríguez-Suárez *et al.* (2010) utilised the model in a study on Tasmanian blue gums (*Eucalyptus globulus* Labill.) in Spain. The model was used to simulate growth of three plots within the same plantation, using height and stem diameter (Rodríguez-Suárez *et al.*, 2010). The model successfully differentiated growth in the three plots based on different site factors (i.e. stocking and fertility rating) and reflect the impact of these factors on height and stem diameter even though they were relatively close together (Rodríguez-Suárez *et al.*, 2010). Rodríguez-Suárez *et al.* (2010) found the model provided highly satisfactory results and showed sensitivity to small-scale site differences, therefore the model was recommended as a tool for forest managers to utilise.

In a study by Dye (2001), the 3-PG model was assessed against the growth and water use of patula pine (*Pinus patula* Schltdl. & Cham.) in four separate sites across a wide geographic range in South Africa. The results of the study were promising in that the model was able to predict realistic long-term simulations of growth and water use for the species across the four sites. However, it was recommended that future studies should include further empirical growth data to improve the accuracy of the model for a more detailed analysis (Dye, 2001). In 2004, Dye *et al.* re-examined 3-PG using 12 stands of hybrid *Eucalyptus grandis*

(W. Hill ex Maiden.) x *Eucalyptus camaldulensis* (Dehnh.) clones of various tree age, growth rates and ecological conditions (Dye *et al.*, 2004). The model simulated growth and water use reasonably well for 11 out of the 12 stands, but the model under-estimated the growth and water use potential of one stand, potentially due to the absence of water stress at the site. The study also recognised the model's limited ability to accurately predict soil water availability and fertility, however, this was potentially a result of the limited information available regarding the environmental and climatic conditions of the sites (Dye *et al.*, 2004).

In Canada, the model was successfully tested by Amichev *et al.* (2010) to simulate the growth of a variety of poplar under Saskatchewan conditions. Walker hybrid poplar (*Populus deltoides* W. Bartram ex Marshall x *Populus nigra* L.) and other short rotation crops are species which can potentially be utilised for bioenergy production (i.e. biomass used for fuel) and other non-commercial benefits such as carbon sequestration (Amichev *et al.*, 2010). Annual data from three poplar sites between 4 to 11 year old stands were used alongside climate and soil data to parameterise the model to the species (Amichev *et al.*, 2010). The study found that the 3-PG model predicted growth to the desired accuracy. Farmers and industries could therefore benefit from this information as there is the potential for the future development of walker hybrid poplar on underutilised agricultural land for financial and environmental benefits (Amichev *et al.*, 2010).

Coops and Waring (2011) conducted a study on lodgepole pine (*Pinus contorta* Dougl.) in the Pacific Northwest of North America. The study found that the sensitivity of 3-PG to seasonal variation enabled the model to identify how the unprecedented rate of future climate change could influence photosynthesis, growth and distribution of the species (Coops & Waring, 2011). The distribution of lodgepole pine was projected to decline by approximately 8% by 2020 and the model projected lodgepole pine would be almost absent from its current geographic range by 2080 (Coops & Waring, 2011). This study highlighted how the model can be used to forecast tree growth under different climate scenarios which could be beneficial to forest managers to manage current plantations and prepare for future challenges which may reduce their distribution.

A variant of the 3-PG growth model has been used to conduct case studies of common and alternative plantation species in Australia, Scotland and New Zealand (Coops *et al.*, 1998; Meason *et al.*, 2011; Meason & Mason, 2014). Coops *et al.* (1998) investigated growth of the dominant forest species across forestry sites within Australia and New Zealand using 3PG-S, which enabled remotely sensed observations as inputs to the model. White cypress pine (*Callitris glaucophylla* J. Thomps. & L. John.), radiata pine and four eucalypt species (*E. pilularis* Sm., *E. maculata* Hook., *E. obliquia* L'Hèr. and *E. regnans* F.Muell.) were modelled to investigate site capacity to grow forests and how climate change would affect the growth response and management of the dominant species (Coops *et al.*, 1998). From one years' worth of data, the model was able to provide a reasonable estimate of the regions ability to grow forests (Coops *et al.*, 1998). Further research by Meason *et al.* (2011) investigated Brown barrel eucalyptus (*Eucalyptus fastigata*) plantations in New Zealand predicting their growth and productivity under different management regimes for a 30 year period. The spatial model of 3-PG_2S was successfully parameterised for the species to generate outputs for stem volume, stem diameter and mean annual increment per hectare for each management scenario (Meason *et al.*, 2011). The integration of the spatial model enabled the outputs to be in the form of GIS (Meason *et al.*, 2011). The study identified soil fertility data as an important feature for the growth of the species at each site, therefore the lack of appropriate soil data affected the accuracy of the model (Meason *et al.*, 2011).

In Meason and Mason (2014), the spatial model was used to simulate the effects of climate change on the future growth of common and alternative plantation species in New Zealand and Scotland. In New Zealand, radiata pine and *E. fastigata* were analysed, while Sitka spruce (*Picea sitchensis* (Bong.) Carrière) and Scots pine (*Pinus sylvestris* L.) were the target species in Scotland (Meason & Mason, 2014). Results from the study found the current climate favoured the common plantation species of radiata pine and Sitka spruce, and a switch to alternative forest species would be disadvantageous to the forestry market in terms of productivity and timber yields (Meason & Mason, 2014). Meason and Mason (2014) concluded that as the potential risks from climate change increase, alternative forest species should continue to be researched to help safeguard the future of plantation forestry.

Similar to other forest growth models, 3-PG has some limitations, as studies have shown the model is limited in its ability to accurately predict the effect of soil hydrology, thinning parameters and fertility (Landsberg & Waring, 1997; Pinjuv *et al.*, 2006). To mitigate this, sub models which specialise in hydrology and fertility can be used to target these weaknesses (Landsberg & Waring, 1997). The 3-PG model has shown promising results from parameterising various forest species around the world and estimating their growth and productivity in variable climatic environments (Pinjuv *et al.*, 2006). The model is generalised, therefore, it is neither site nor species specific, so can be parameterised to various species including alternative forest types such as indigenous forest species like tōtara (Landsberg *et al.*, 2003). Validation of the model is crucial to ensure the model is the right fit for the specified target species/forest type, and to determine whether the model can provide accurate estimates of growth for other sites which were not used for calibration (Vanclay & Skovsgaard, 1997; Pinjuv *et al.*, 2006).

1.3.4 Modelling tōtara

The growth, survival, distribution, potential timber yields and silvicultural management of tōtara in New Zealand have been examined in earlier studies but, there have been few attempts to model growth and yield (Bergin, 2000; Bergin & Kimberley, 2003; Simpson, 2017; Dowling & Steward, 2018). The growth and survival of planted tōtara stands is dependent on the location of planting, therefore, having the ability to forecast growth in new locations would be highly beneficial for landowners and forest managers, to help enhance growth and ensure the appropriate stand density. Limited data, harvest restrictions and a lack of interest from researchers have prevented the development of accurate growth and yield models for tōtara (Bergin, 2000; Bergin & Kimberley, 2003; Simpson, 2017). Although tōtara is distributed over a wide range of environments across the country, only a limited number of permanent sample plots (PSPs) have been established. Process-based models like 3-PG can utilise small datasets and have the potential to be used as research tools to provide the data needed to inform management decisions (Pinjuv *et al.*, 2006). Furthermore, studies on the growth of tōtara can be advantageous to the limited knowledge base on the species (Höck *et al.*, 2017; Lin *et al.*, 2018).

A review by Höck *et al.* (2017) identified that there was limited information regarding the carbon sequestration rates and optimal growth conditions of less common species like tōtara that are potentially highly suitable for carbon forestry. Studies on tōtara have primarily focused on modelling timber yield using empirical models to help with management decisions (Bergin & Kimberley, 2003). Bergin and Kimberley (2003) made the first attempt to predict growth and yield of tōtara by developing height/age curves and diameter/age curves from mensuration data collected from thirteen sites across the North Island. The tōtara stands were measured in the mid-1980s and measurements were repeated approximately 12 years later to formulate a growth analysis (Bergin & Kimberley, 2003). The height/age curves were calculated from the mean heights of stands (estimated and measured), whereas the diameter/age curves were from mean diameters and core measurements (Bergin & Kimberley, 2003). Statistical growth functions which are commonly used in forestry growth equations were incorporated into the height and diameter equations to improve the accuracy of the predictions (i.e. Chapman-Richards function) (Bi *et al.*, 2000; Bergin & Kimberley, 2003).

The study found height growth was rapid over the first 25 – 30 years since planting (Bergin & Kimberley, 2003). Linear trends in diameter growth of the species were observed, providing estimates for stem diameter between 20 cm to 100 cm depending on the age of the stand (Bergin & Kimberley, 2003). Most of the stands lacked sufficient after planting care and management and stands were found growing in unfavourable conditions, therefore resolving these issues could improve the growth of the species substantially (Bergin & Kimberley, 2003). Bergin and Kimberley (2012) added further information to the knowledge base of tōtara by conducting a study to estimate the age of natural and regenerated tōtara stands using wood cores. An earlier study from Hinds and Reid (1957) identified how the growth rings of tōtara are not easily defined. Bergin and Kimberley (2012) identified that quality checking wood cores to remove the cores with irregularities improved age estimates (Bergin & Kimberley, 2012). The study found that the latewood band counting method provided reasonable estimates of the age of tōtara in planted stands and could potentially be used in future studies to identify the age of trees (Bergin & Kimberley, 2012).

In addition, a suitable volume equation for tōtara does not currently exist. Previous studies have referred to the indigenous volume equations by Ellis (1979). The equations for rimu were predominately used due to the longevity and site preferences of the species (Ellis, 1979). Bergin and Kimberley (2003) used the kāuri pole stand equation from Ellis (1979) due to the similarities in height and diameter values of kāuri. Biomass studies on the species are also limited as without destructive harvests of tōtara individuals, the tree masses are rather difficult to quantify (Bergin *et al.*, 2008; Höck *et al.*, 2017; Marden *et al.*, 2018). Previous attempts to understand the biomass of tōtara have been conducted on juvenile tōtara seedlings (0-5 years after planting), however, due to the longevity of the species, the results from the study could not be extrapolated to estimate the biomass of young adult and mature tōtara (Marden *et al.*, 2018).

1.4 Summary

The future of forestry in New Zealand relies heavily on the ability of landowners and forest managers to accurately predict growth of indigenous forest species, and how this might change in response to climate change. The ETS and OBT programme have substantially increased the demand for further research on indigenous forest species. These species can help offset greenhouse gas emissions when utilised as carbon forests or provide sustainable timber resources. Tōtara is one of these key species which has the potential to provide commercial, cultural and economic benefits, however, research on the species and its projected growth is constrained by limited data. The parameterisation of tōtara to 3-PG could substantially improve predicted growth and yield information on the species. This information could improve the knowledge base available for managing planted and naturally regenerated tōtara stands.

1.5 Research Aim and Objectives

The aims of this thesis are to identify the main drivers of productivity of tōtara across the North Island and to model this growth with 3-PG.

To achieve this, three objectives were set:

1. Measure site-specific growth across different sites and investigate which physiological and environmental variables are the main productivity drivers for tōtara.

2. Quantify growth at each site in preparation for calibration and validation of the 3-PG forest growth model.
3. Calibrate the 3-PG model and validate the fitted model against an independent dataset to investigate the performance of the model at predicting productivity of tōtara.

1.5.1 Thesis structure

This thesis consists of four chapters: Chapter one reviews previous research on tōtara and forest growth models. It identifies key knowledge gaps and the importance of further research on indigenous tree species that might be suitable to offset greenhouse gas emissions or to produce sustainable timber harvests.

Chapter two focuses on site productivity and growth of tōtara across planted and naturally regenerated stands in the North Island. This chapter will identify the climatic and environmental variables which influence the productivity of tōtara. In addition, growth across sites will be quantified in preparation for calibration of 3-PG.

Chapter three outlines the calibration and validation of the 3-PG model to tōtara. It identifies key productivity drivers of the species and how well the 3-PG model was able to predict growth for the species.

Chapter four synthesises the main conclusions from this thesis in a general discussion. The findings from this thesis will be discussed in relation to current scientific literature and recommend ideas for future research.

Chapter 2

Site Productivity

2.1 Introduction

Worldwide, forests are influenced by a combination of interacting abiotic and biotic factors to support tree growth (Skovsgaard & Vanclay, 2008; Weiskittel *et al.*, 2011). As the pressures from climate change increase, research into forest ecosystems and their management is becoming more prevalent (Schenk, 1996; Weiskittel *et al.*, 2011). It is however currently unknown how climate change will affect forests and the species within them, unsettling forest owners and managers. Projections are that the survival and distribution of forest species may be adversely affected in future climate situations (Schenk, 1996; Kirilenko & Sedjo, 2007). Climate change is projected to alter temperature and rainfall patterns and increase the frequency and intensity of forest fires and disease (Kirilenko & Sedjo, 2007). Therefore, it is crucial for forest management to prepare for these changes (Schenk, 1996; Loehle, 2000; Kirilenko & Sedjo, 2007). Research to date has focused on identifying different management approaches by collecting forest mensuration data from research trials and modelling their future productivity. However, the vast majority of this research lacks site and soil productivity information, which could help identify key growth limiting factors which effect the survival and productivity of forest species. A better understanding of the biological, chemical, environmental and physiological factors influencing growth can improve the accuracy of modelling attempts, help with silvicultural management decisions and be used to identify suitable areas to plant trees required to meet the demands for commercial and non-commercial forestry.

Research focused on forest species has demonstrated that all species of trees require sunlight, carbon dioxide, water, nutrients and appropriate temperatures to survive (Callaham, 1962; Louw & Scholes, 2002; Toledo *et al.*, 2011; Weiskittel *et al.*, 2011; West, 2014). The availability of these fundamental resources over spatial and temporal scales can limit or accelerate growth by adjusting the individual trees metabolic and photosynthetic rates (Toledo *et al.*, 2011). Soil fertility, temperature and rainfall are the main climatic and environmental factors which form the

microclimate of sites (Pretzsch, 2009; Weiskittel *et al.*, 2011; West, 2014). The relationship between the growth limiting resources and environmental conditions of a site can shift when one or more of the resources are abundant or limited (West, 2014). The potential effects of this on productivity are specific to each species genetic, physiological and structural adaptations to their growing environments and their range of tolerance to fluctuating environmental conditions (Callaham, 1962). For example, increased temperatures from climate change could see many tree species face reduced geographical distributions as temperatures increase beyond the species tolerance level (Saxe *et al.*, 2001; West, 2014). Tree species are generally well adapted to daily and seasonal fluctuations (Saxe *et al.*, 2001; West, 2014). However, when temperatures fall above or below optimal growth conditions for long durations (e.g. periods of drought or frosts) the photosynthetic rate of the trees can be affected, impacting their survival (Callaham, 1962; Saxe *et al.*, 2001; West, 2014). Tree geographic distribution is also influenced by soil type and other non-climatic factors, however, the level of influence from these factors is unknown for most species (Kirschbaum, 2000). Common tree species used predominantly in plantation forests have been well studied, however for indigenous tree species we lack this key information (Höck *et al.*, 2017; Lin *et al.*, 2018).

As pressures from climate change continue to threaten the future of forest ecosystems, research has become a vital component to protecting plantation and indigenous forest species. Over the last twenty years, there has been a rise in the demand for more information about indigenous tree species and their productivity to help offset greenhouse gas emissions through carbon storage (Höck *et al.*, 2017; Lin *et al.*, 2018). These indigenous forests can be managed to increase carbon sequestration and to accelerate growth of individual trees which could be selectively logged for timber (Landsberg & Sands, 2011). However, without the knowledge of the biological, chemical and physical interactions occurring between the indigenous trees and their environment, landowners and forest managers will struggle to successfully manage these forests for economic, social and environmental gains.

Site productivity is one of the key criteria used globally by forest managers to help resolve the uncertainties regarding the future growth, production and profitability of forests (Richardson *et al.*, 1999). The term ‘site’ is used in forestry in reference to an area of land under homogenous conditions that can be managed to produce a

predictable wood yield (Skovsgaard & Vanclay, 2008; Weiskittel *et al.*, 2011; West, 2014). Skovsgaard and Vanclay (2008) defined productivity as the sites' maximum ability to support the total biomass of a particular species (Skovsgaard & Vanclay, 2008; Landsberg & Sands, 2011; Weiskittel *et al.*, 2011). Each site consists of complex biological, chemical and physiological factors which influence growth and productivity within the prescribed area (Louw & Scholes, 2002; Skovsgaard & Vanclay, 2008; Weiskittel *et al.*, 2011; Salekin *et al.*, 2019). Growth can be defined as the increase in stem diameter and height of an individual tree (Pretzsch, 2009). By identifying the factors which can influence the productivity of a species at the site, for example soil chemistry properties and competition, forest managers can design management strategies to optimise or accelerate growth (Pretzsch, 2009; West, 2014). These strategies include the use of silvicultural techniques which include the use of chemical fertilisers, vegetation control, and pruning and thinning operations (Burger & Kelting, 1999). To measure the effects of these techniques, forest managers need to find accurate and effective ways to measure stand and site productivity (Skovsgaard & Vanclay, 2008; West, 2014).

Site productivity can be measured by site index proxies (Skovsgaard & Vanclay, 2008; Weiskittel *et al.*, 2011; Bontemps & Bouriaud, 2013). Site index measurements are derived from forest stand estimates which identify the dominant height of the stand at a reference age (Skovsgaard & Vanclay, 2008). This proxy requires site specific empirical data from homogenous stands to form the height vs age relationships (Burkhart & Tennent, 1977; Skovsgaard & Vanclay, 2008). The index can be used for general estimates of site productivity in similar growing conditions around the region. For the dominant plantation species, this information is easy to obtain and has been thoroughly researched over the last half century (West, 2014). However, for indigenous tree species this information is limited (Bergin, 2001; Lin *et al.*, 2018).

2.1.1 Site productivity for tōtara

Tōtara is one of the indigenous tree species which could benefit greatly from further research surrounding the factors driving productivity (Höck *et al.*, 2017; Lin *et al.*, 2018). The early exploitation of indigenous tree species in New Zealand, combined with the effects from natural and anthropogenic disturbances (e.g. land clearance

and fire) reduced the population size available for wood supply, therefore, restrictions were put in place (Bergin & Kimberley, 2003; Allen *et al.*, 2013). After years of legal protection to conserve the current forests and prevent logging, indigenous tree species are being researched to identify their suitability for timber and carbon forestry (Lin *et al.*, 2018). Over the years, landowners have kept natural groves of tōtara or planted them for a variety of reasons (e.g. erosion control and biodiversity) in mixed or homogenous stands (Bergin, 2000, 2001; Simpson, 2017). This has created a growing interest to utilise them for timber or carbon forestry to generate financial benefits from the species (Bergin, 2000). Literature has briefly touched on understanding the growing conditions and tolerance of the species, however, no conclusive relationships have been identified between the productivity of tōtara and the specific site variables enabling growth (Höck *et al.*, 2017; Lin *et al.*, 2018).

Previous research from literature identified that tōtara trees can be found across a wide geographic distribution and are commonly found in the warmer climatic regions of the North Island (Hinds & Reid, 1957; Bergin, 2001; Simpson, 2017). However, the species is also present in the South Island where the mean annual temperature is colder than the North Island (Hinds & Reid, 1957). Furthermore, studies have found tōtara trees to be tolerant of frost but their level of tolerance is largely dependent on the age of the individual and the intensity of the frost (Hinds & Reid, 1957; Simpson, 2017). Mature tōtara trees can tolerate frosts more than seedlings which may struggle to survive in the cold conditions (Beveridge, 1962; Bergin, 2001). Specifically, Beveridge (1962) studied the growth and survival of native podocarp seedlings and found that tōtara seedlings were able to withstand periodic frosts which occur during the winter (Beveridge, 1962; Simpson, 2017). However, unseasonable frost events were found to harm the growth of young seedlings and have made it difficult to identify the optimal environmental conditions and temperatures suitable for the growth of tōtara after seedling establishment (Hinds & Reid, 1957; Hawkins, 1988; Simpson, 2017).

On the opposite side of the spectrum, tōtara is thought to be tolerant of dry conditions but intolerant of oversaturated conditions (Hinds & Reid, 1957; Simpson, 2017). Similar to frosts, high intensity or long duration drought stress can cause individual tree mortality (Hinds & Reid, 1957; Wardle, 1985; Bergin, 2003a;

Simpson, 2017). The species grows on a range of soil types around New Zealand, however, studies have shown that the species grows best in well drained lowland and pumice soils (Hinds & Reid, 1957; Bergin, 2003a). Waterlogged or badly aerated soils are poor environments for tōtara to grow in (Marden *et al.*, 2018). The soil properties of alluvial flats enable water to drain away as the grain sizes are large or perforated (e.g. gravel and pumice) (Simpson, 2017). Tōtara is often found growing on these soils, therefore, drainage is most likely important for growth. Ultimately, there is little quantitative information about the types of soil and level of soil fertility preferred by tōtara. It is known tōtara tends to grow on lowland and alluvial soil types which are fertile, but it is not known what concentrations of each are optimal for growth.

There are potentially many interacting factors which determine the distribution and growth of tōtara in various areas around New Zealand. Common themes retrieved from literature suggest that tōtara does best in well-lit environments on fertile, well-drained soils (Hinds & Reid, 1957; Hawkins, 1988; Bergin, 2003a; Simpson, 2017). It is however unknown what other factors may be influencing the productivity of the species. As such, understanding and measuring forest site productivity is crucial to improve growth and yield models and to help inform decision making and management (Marshall *et al.*, 2015). This data could be used to identify methods to increase initial survival rates of seedlings and wood production, while identifying future sites for afforestation where the species can be planted for timber and carbon forestry.

2.2 Objectives

The purpose of this study was to outline the selection of representative study sites to explore the relationship between site variables and tōtara productivity in the North Island of New Zealand. A further objective was to quantify growth at each site in preparation for calibration and validation of the 3-PG forest growth model in Chapter 3. It was hypothesised that site fertility and temperature would be significant drivers of productivity.

2.3 Methods

2.3.1 Databases

Three databases provided information on measured tōtara stands within New Zealand (Figure 2.1). These databases were the Permanent Sample Plot (PSP) database managed by Scion, the Land Use and Carbon Analysis System (LUCAS) database controlled by the Ministry for the Environment (MfE), and Field Management Approach (FMA) database controlled by Ministry of Primary Industries (MPI). Access to the information in these databases were provided by Scion and MfE.

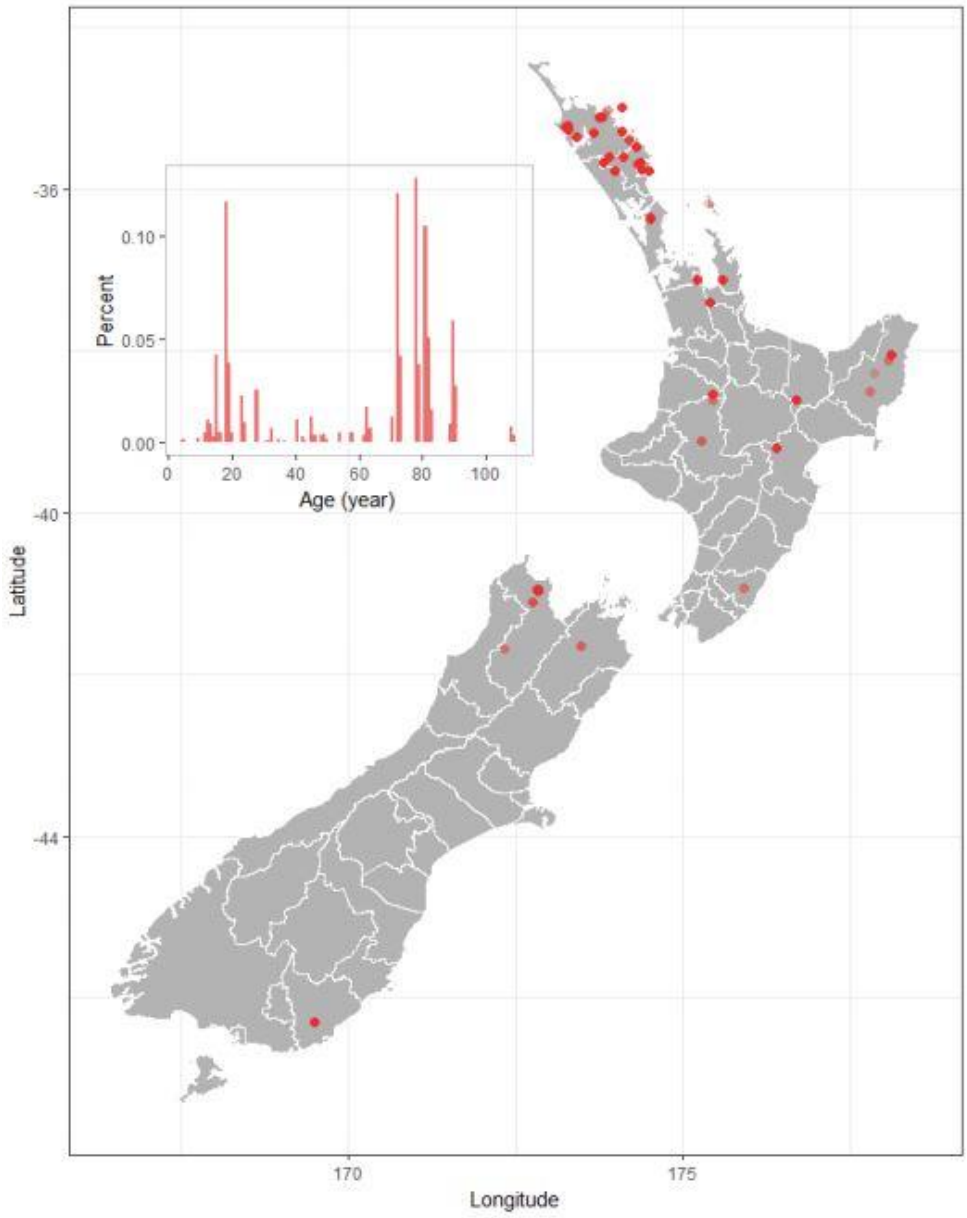


Figure 2.1. Distribution of tōtara stands and age range for forest measurements around New Zealand from PSP, LUCAS and FMA Databases (Lin *et al.*, 2018).

2.3.2 Selection of study sites

All sites from the databases were located on Land Information New Zealand (LINZ) Topo50 Map using their GPS coordinates to determine their geographic location. All selected sites were located in the North Island, New Zealand. Representative sites were chosen from the limited number of plots available. Fifteen sites were selected in this study to calibrate the 3-PG model (Figure 2.2 & Table 2.1). Mean annual total rainfall (mm) and mean annual temperature (°C) for each site were retrieved from the Virtual Climate Stations Network (VCSN) (Table 2.1). The majority of the study sites were situated on private land, therefore, to keep the data and location of the stands confidential, site descriptions and data are identified by site number (1-15) and region (Figure 2.2 & Table 2.1).

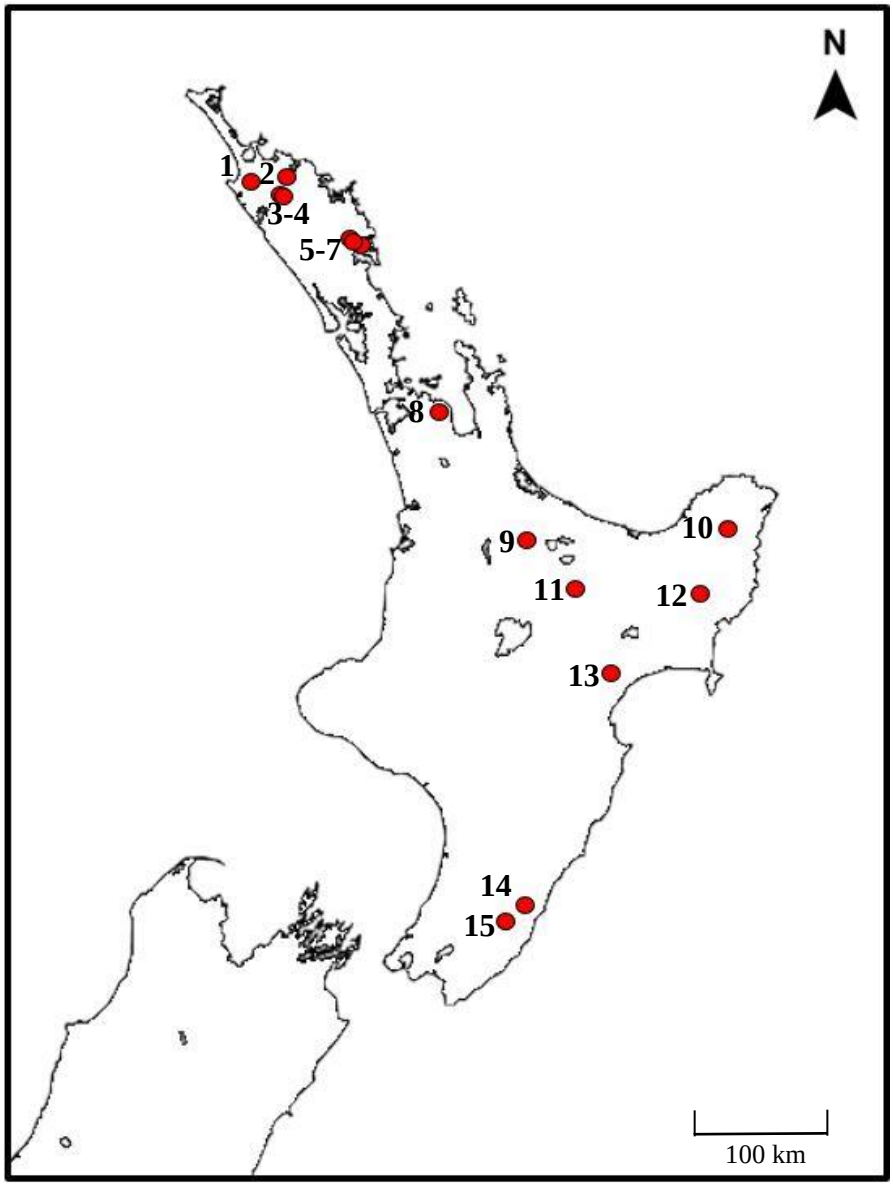


Figure 2.2. Location of the 15 sites from the North Island, New Zealand, used to calibrate the 3-PG growth model for tōtara.

Table 2.1. Summary of the fifteen study sites used for calibration. Age of the sites is for the year 2019. Min: minimum; Mean: ± standard error; Max: maximum; Mean temperature and Mean total rainfall are annual values.

						DBH (cm)			Height (m)				
Site	No. Plots	Size (ha^{-1})	Stocking (stems ha^{-1})	Age (years)	Elevation (m)	Min	Mean	Max	Min	Mean	Max	Mean temp (°C)	Mean total rainfall (mm)
1	3	0.03	731	84	116	14.17	15.56 ± 1.23	18.01	9.30	10.25 ± 0.61	11.39	14.63	1626.69
2	3	0.03	1462	84	41	16.12	20.03 ± 2.28	24.02	11.94	14.40 ± 2.06	18.50	14.04	1885.11
3	3	0.02	667	89	54	16.38	21.68 ± 2.74	25.5	12.40	14.80 ± 1.61	17.86	14.26	1484.17
4	2	0.03	1387	89	265	14.86	15.08 ± 0.23	15.31	9.76	9.84 ± 0.09	9.93	14.26	1484.17
5	3	0.04	578	69	160	23.09	29.07 ± 3.27	34.37	13.67	13.89 ± 0.19	14.28	14.71	1633.01
6	3	0.03	1236	119	133	21.09	37.38 ± 10.88	58.02	16.95	21.20 ± 2.22	24.46	14.68	1625.47
7	3	0.03	1710	101	64	16.58	18.61 ± 1.73	22.05	10.36	12.90 ± 2.37	17.63	15.07	1473.02
8	8	0.05	2183	30	40	12.68	14.42 ± 0.31	15.48	10.42	10.92 ± 0.09	11.22	13.44	1206.23
9	4	0.04	316	60	561	17.40	20.75 ± 1.60	25.08	11.94	12.87 ± 0.35	13.66	10.57	2287.47
10	3	0.03	417	120	392	27.72	41.63 ± 7.71	54.37	12.33	17.60 ± 2.64	20.50	12.04	1709.79
11	3	0.03	831	60	541	16.33	18.24 ± 1.54	21.3	11.75	12.56 ± 0.40	13.02	10.44	1391.54
12	3	0.03	935	72	150	24.89	26.15 ± 0.91	27.91	15.94	16.65 ± 0.36	17.11	12.89	1069.00
13	3	0.04	1652	86	248	17.69	19.93 ± 1.31	22.21	12.63	14.07 ± 1.00	16.00	12.14	1544.68
14	3	0.03	1197	80	137	17.81	27.75 ± 5.89	38.19	10.88	15.27 ± 2.20	17.56	12.36	1280.25
15	4	0.05	747	10	204	3.17	5.04 ± 1.51	9.55	2.25	2.76 ± 0.39	3.92	12.00	1013.76

2.3.3 Stand and site descriptions

Permanent Sample Plots (PSPs) in both planted and naturally regenerated tōtara stands were measured for this study. All tōtara stands used in this thesis had a history of measurement prior to this study. The previous site history and data were retrieved from the PSP database, MfE, landowners and forest managers. Ages of the stands ranged from 10 – 120 years old, with an average age of approximately 60 years old. Stand descriptions include the site history of the stand and whether silvicultural regimes have been used. Most of the naturally regenerated stands occurred on hill slopes which had previously been cleared for pasture.

2.3.3.1 Site 1 - Northland

This site is located north of Herekino on private farmland (Figure 2.3). The tōtara stand is situated on a hill slope across from a small stream. Naturally regenerated second growth tōtara trees dominated the stand along with kānuka trees. Originally, 3 PSPs were established at this site as part of a research trial to examine silvicultural regimes (e.g. control, thinning and pruning) (Bergin, 2001). These PSPs were remeasured using 12 metre circular plots.

Figure 2.3. Site 1 at age 89, with tōtara and kānuka trees growing on a steep hillslope in Northland.

2.3.3.2 Site 2 - Northland

A series of PSPs were previously established at this site to trial silvicultural regimes, including thinning (Bergin, 2001). This site is located south of Kaeo on private farmland. Three PSPs with naturally regenerated tōtara were remeasured. Two PSPs are in a grove of tōtara which is not fenced off from stock and other animals. The other PSP was formed on a steep hillslope adjacent to a small farm stream. Stock has been excluded from the stand. The understory vegetation throughout the PSPs varied, with the thinned plots having the densest understory vegetation.

2.3.3.3 Site 3 - Northland

This site is dominated by naturally regenerated tōtara. The PSPs are located on private farmland just below the Waihou River to the north east of Horeke. The PSPs were previously established to trial silvicultural regimes and were scattered above and below rocky outcrops on the property (Bergin, 2001).

2.3.3.4 Site 4 - Northland

This site has two PSPs located on private farmland, overlooking the Waihou River (Figure 2.4). The PSPs are on a sunny hillslope surrounded by rocky outcrops and were previously established as part of a trial of silvicultural regimes (Bergin, 2001).

Figure 2.4. Naturally regenerated tōtara stand located at Site 4, growing below a rocky outcrop on a moderate hillslope.

2.3.3.5 Site 5 - Northland

This stand of tōtara is located within a large planted forest located north of Whangarei. Tōtara trees were planted in 1952 at this site on a gentle to steep hill slope (Bergin, 2001). Tree ferns (*Cyathea dealbata* (G. Forst.) Sw.) were the main vegetation present beneath the tōtara. Little silvicultural management has occurred within the tōtara stand apart from early weed releasing.

2.3.3.6 Site 6 - Northland

This site is located 12 km north of Whangarei. The tōtara trees at this site were naturally regenerated. The rest of the site is planted in exotic forest types. The PSPs had a range of stockings, ages and silvicultural treatments (Figure 2.5) (Bergin, 2001). There was little competition between other species at this site, as the PSPs were dominated by tōtara. Stock have not been excluded from this site.

Figure 2.5. Two of the PSPs located at Site 6 in Northland. Left image shows tōtara growing on a steep hillslope at the top of a ridge. Right image shows tōtara growing at the bottom of a wide valley.

2.3.3.7 Site 7 - Northland

This site is located on a private property overlooking Whangarei Harbour. A series of PSPs were previously established at this site to trial silvicultural regimes (Bergin, 2001). Three PSPs at this site were remeasured. Two of the PSPs are located on a steep hillslope, while the other is located at a lower elevation on a gentle hillslope. The tōtara stands where the PSPs were established were not fenced to exclude stock.

2.3.3.8 Site 8 - Auckland

This planted stand is located to the south east of Auckland and borders the Firth of Thames (Figure 2.6). The coastal site was previously pastoral land before it was planted in 1989. Eight plots (0.0576 ha) were established as part of a provenance trial investigating variation in tree growth and form (Bergin, 2001; Bergin *et al.*, 2010). The site has a history of monitoring and management, including releasing the plants from weeds and stock exclusion by fencing (Bergin, 2001).

Figure 2.6. One of the eight planted PSPs at Site 8 in the Auckland region.

2.3.3.9 Site 9 - Bay of Plenty

This site was originally a tawa forest (27.92 ha) until tractor cleared gaps were made to establish a podocarp seedling trial (Pardy, 1983). The tōtara trees in this forest were planted as seedlings in 1961 along with kahikatea and rimu (Pardy, 1983; Bergin, 2001). The topography is relatively flat, with small mounds and tomo holes. Four PSPs were established in areas of the forest where tōtara were the predominant species present.

2.3.3.10 Site 10 - East Cape

Three PSPs were established in a private forest, in the Te Puia Springs area, north of Gisborne. The tōtara trees have naturally regenerated in this site in the riparian zone of a small stream which flows through a gully. The tōtara trees along this gully were surrounded by plantations of pine trees. No silvicultural treatments have been used at this site previously.

2.3.3.11 Site 11 -Waikato

The tōtara at this site were originally planted under a 36 year old ponderosa pine (*Pinus ponderosa* Dougl. ex Law.) forest, along with rimu and kahikatea (Dacrycarpus dacrydioides (A.Rich.) de Laub.) in 1962 (Pardy, 1987). The pines provided a slightly sheltered canopy to protect the species from the cold frosts in this upland site, which is close to the species maximum elevation of 550 metres above sea level (asl). The trees were planted in lines underneath the *P. ponderosa* canopy with a spacing of 3.6m x 1.8m (Bergin, 2001). Three 0.031ha plots were established in the tōtara dominated areas. The *P. ponderosa* trees were unhealthy from *Dothistroma pini* infection therefore, the understory vegetation was quite dense in some areas with tree ferns, blackberry and flax. No silvicultural treatments have been applied in any of these stands as the site was left largely untouched. The site is relatively flat and is frequently affected by heavy frosts.

2.3.3.12 Site 12 - East Cape

Three PSPs were established in a naturally regenerated tōtara stand northwest of Gisborne. This tōtara stand is located on private farmland and there are various naturally regenerated tōtara groves spread across the site. This stand has previously been thinned and had temporary fencing around it to exclude stock (Figure 2.7).

Figure 2.7. Naturally regenerated tōtara stand located at Site 12. This stand had been thinned to manage the growth and form of the trees.

2.3.3.13 Site 13 - Hawkes Bay

A 0.5 ha stand of tōtara was planted at this arboretum located 40 km northwest of Napier. This stand was planted at 1.5 m to 3 m spacing, adjacent to a stand of planted kauri (Bergin, 2001). Two plots were located in this tōtara stand on a gentle hill slope (Bergin, 2001). These two plots were pruned and due to the density of the trees, little understory vegetation was present. The third plot was located on a steep hill slope above a stream at the back of the arboretum. This plot had a small mix of understory vegetation compared to the other two plots. Since the arboretum is managed, stock were excluded from the arboretum to prevent damage to the trees.

2.3.3.14 Site 14 - Wellington

This site is located on private farmland in the Wellington region. The tōtara at this site is found growing either side of a small stream in the riparian zone. The stand is predominately naturally regenerated tōtara, with a mix of mānuka and kānuka present. There is a small mix of understory vegetation, mainly saplings. Stock are excluded from the stand.

2.3.3.15 Site 15 - Wellington

This site is located approximately 23 km east of Masterton on a property owned by a charitable trust. The four tōtara plots at this site were planted in 2006 in different light conditions, ranging from plots in full light, partial shade and full shade (Meason *et al.*, 2019). The understory vegetation at each of the plots differed depending on the amount of light available and size of the trees. At plots where growth was small, understory vegetation was high, whereas at plots where the tōtara trees were taller and were close to canopy closure, the understory vegetation was limited to grasses. This site is vulnerable to grazing by stock and deer as there is no fencing on the property. There has been little management of the site apart from weed management after planting. The plots were measured annually since planting to analyse their growth performance (Meason *et al.*, 2019).

2.3.4 Access to sites

The accessibility of the sites varied between locations and ownership. For privately owned forests, the landowners were contacted prior to arrival to gain verbal and/or written permission to access and measure the site. Sites which where owned by forest companies or managed by government organisations were contacted accordingly through a representative from the company to receive permission.

2.3.5 Plot establishment

At each site, 3 PSPs were created to collect representative tree mensuration data. Topography, size of the stand, stand density and vegetation were key factors used to determine the size and location of each plot within the stand. A minimum of 16 trees were required in each PSP to provide sufficient data for each site. Circular plots were used due to their ease of establishment. For plots with high stand densities (e.g. 3000 stems ha^{-1}) 10 m diameter plots were used (Table 2.2). For sites with low stem densities (e.g. 200 stems ha^{-1}) 12 m diameter plots were used. At sites where the stand density was extremely low (e.g. $\leq$ 100 stems ha^{-1}) 8 m diameter plots were used to reduce inclusions of non-target trees (Table 2.2). Where possible, the plots had buffer trees on the outside of each plot to prevent plots overlapping and reduce edge effects in this study. For Site 8 and Site 15, all trees were measured within the plots at the original plot size that was established.

For the PSPs which were unable to be located by GPS, the new PSPs were established as close to the original coordinates as possible. Previous silvicultural history and measurements could then be used for these sites. When only one PSP existed at a site, two additional PSPs were established and marked to ensure a representative dataset was retrieved from each growing site. The Haglöf vertex (IV) ultrasonic hypsometer and transponder were used to determine the plot boundary. GPS coordinates were recorded from the centre of each PSP and each tōtara tree was numbered in a clockwise direction in an order determined by compass bearings to help with future remeasurements. This followed the protocol for PSP establishment from Ellis and Hayes (1997). Centre pegs were left in each PSP to help locate the PSPs which were unable to be marked with spray paint to help with future remeasurements.

Table 2.2. The size of circular Permanent Sample Plots (PSP) which were established and measured at each site.

Diameter (m)	Size (m^2)	Size (ha^{-1})
8	201	0.020
10	314	0.031
12	452	0.045

2.3.6 Field Measurements

The following field measurements were recorded from the 15 calibration sites between February and September 2019.

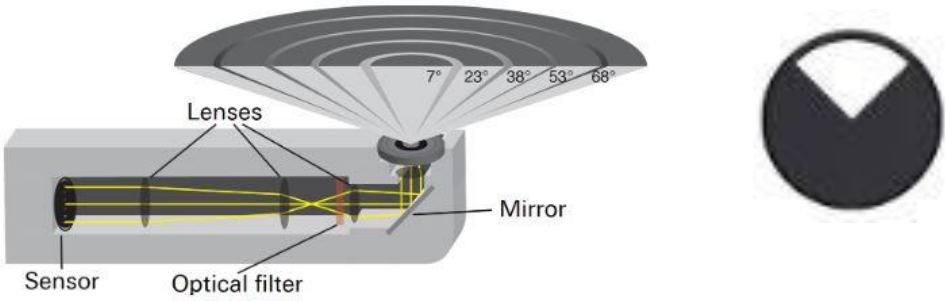
2.3.6.1 Growth measurements

Following the protocol from Ellis and Hayes (1997), tree height (m) and stem diameter (cm) were collected from tōtara trees located within each PSP. The diameter at breast height (DBH) of all trees was measured at 1.4 m above ground, on the uphill slope to standardise measurements. If the stem of the tōtara had an irregularity at DBH, the measurement was shifted to above or below the irregularity to reduce errors. All individuals with a DBH equal to or more than 1.5 cm were measured within the plot. Heights were measured using a Haglöf vertex (IV) ultrasonic hypsometer and transponder. In each plot a minimum of 12 height trees were selected. In PSPs with a high number of stems, the top 1/3 of all DBH measurements were chosen as height trees to represent the general trend within each plot.

2.3.6.2 Leaf Area

A Licor 2200C canopy analyser was used to measure the Leaf Area Index (LAI) in each PSP (Figure 2.8). LAI can be defined as the foliage area index which represents the amount of foliage (m^2) per unit of ground surface (m^2) (LI-COR Biosciences, 2019). The wands (A & B) were calibrated before data collection to ensure the timing of each reading and sky conditions were similar. A 90° view cap was used on each wand to limit the field of view (Figure 2.8). This enabled the lens to only measure within the boundaries of the plot and reduced inclusions of non-target trees. The A wand was set to auto-log to record the sky conditions over the

measurement period. This was set in an open area, away from any shadows or objects/animals which may have obscured the lens and blocked the light (Figure 2.9).



a. **b.**

Figure 2.8. a. Design of the Licor 2200C canopy analyser sensor. 8b. The 90° view angle cap for the canopy analyser (LI-COR Biosciences, 2019).

Figure 2.9. LAI A Wand measuring sky conditions.

In each PSP, the B wand was used to acquire 12 point measurements beneath the tōtara canopy. To ensure an accurate representation of the canopy, one measurement was taken at each of the eight cardinal and ordinal positions around the outer boundary of the PSP, moving in a clockwise direction, and facing the wand towards the centre of the plot (Figure 2.10a). Cardinal measurements (North, East, South and West) were then taken above the centre peg, facing towards the outer boundary of the plot (Figure 2.10b).

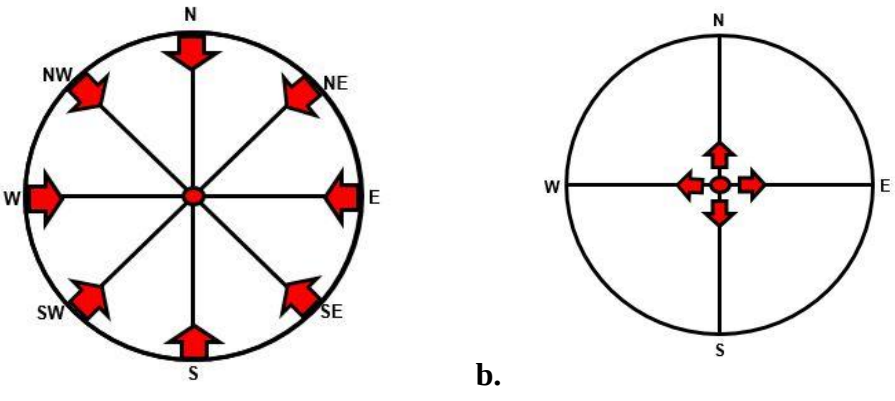


Figure 2.10a. Diagram of how leaf area was measured using LICOR canopy analyser. Point measurements began at the outer boundary of the PSP, facing towards the plot centre. Measurements were then acquired in a clockwise direction. b. Diagram of leaf area measurements taken from the centre of the PSP facing towards the outer boundary.

In plots where the understorey vegetation prevented a clear view of the canopy, LAI data were not obtained. To help reduce errors regarding the sky conditions at the time of sampling, scatter files were used. When the weather conditions were sunny with cloud cover, scatter files were created before and after analysing the canopy to reduce the amount of error while sampling. Data from each site were combined for further analysis. These readings were processed later using the FV2200 software.

2.3.6.3 Soil properties

A portable ground conductivity sensor called the Dualem-1 (Dualem Inc. Canada) was used to measure the apparent electrical conductivity of the soil (EC_a) to identify spatial variations in soil properties (e.g. water content, salinity, and soil textural layers) (Figure 2.11 & Figure 2.12) (Grisso *et al.*, 2005; Doolittle & Brevik, 2014; Dualem Inc, 2014). The sensor simultaneously measures the EC_a at two depths using an electromagnetic transmitter and two receivers. These receivers are the horizontal co planar geometry (HCP) and perpendicular geometry (PRP) which take horizontal and vertical measurements of the soil. The HCP receiver analyses the soil to depths of 1.5 m, whereas the PRP receiver reaches depths of 0.5 m (Doolittle & Brevik, 2014; Dualem Inc, 2014). The electrical conductivity is expressed in units of milliSiemens per meter (mS m^{-1}) (Figure 2.11) (Grisso *et al.*, 2005).

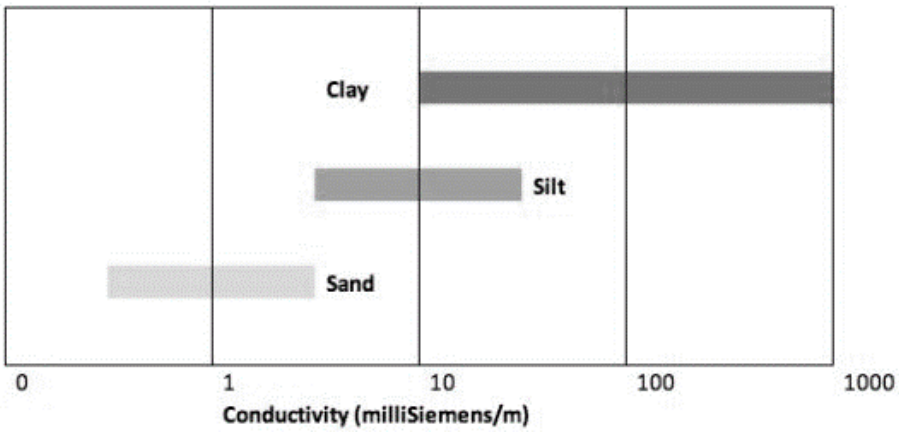


Figure 2.11. Relationship between soil textural properties and soil electrical conductivity (mS m^{-1}) (Grisso *et al.*, 2005).

The Dualem-1 sensor was calibrated before and after the measurement period to account for any environmental changes which may have occurred during field measurements. Once at ambient temperature, 36 point measurements were taken from the atmosphere at 10° increments as the sensor was rolled 360° while remaining parallel to the ground (Figure 2.12). Calibration pipes were used to elevate the sensor to approximately 1.6 m to avoid soil influence.

Figure 2.12. Dualem-1 sensor in use measuring a PSP.

To acquire a measurement the sensor was placed directly on bare ground, to reduce the effects of vegetation or wood impacting the pulse. In each PSP, point measurements were recorded at approximately 2 m intervals along 4 measurement lines to ensure a representative sample was acquired from the PSP (Figure 2.13).

Due to the small size of the plots, taking point measurements every few metres enabled a representation of the variation in soil physical properties. Where possible metal, vegetation and dead branches were avoided to ensure an accurate measurement was recorded.

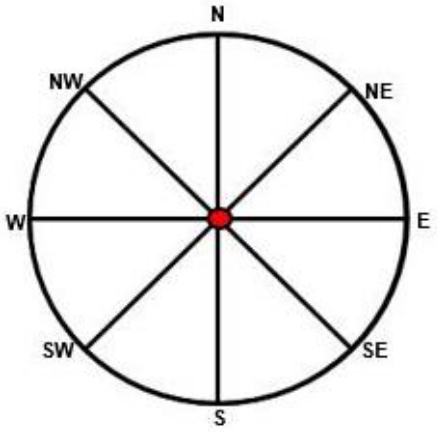


Figure 2.13. The four measurement lines used with the Dualem-1 sensor to take point measurements within the PSP at two metre intervals.

Data were downloaded from the Dualem-1 using duupload.exe. Data from each site were cleaned using Minitab 19 to remove any anomalies.

2.3.6.4 Soil samples

Soil samples were collected from each PSP for chemical analysis from 0 – 10 cm depths using a modified stainless-steel soil Hoffer sampler (2.3 cm diameter) (Figure 2.14). Overlying organic matter was scraped away prior to taking each core. The samples were collected across each plot from random locations. Approximately 16 samples per plot were bulked together in a clean plastic bag and labelled for laboratory analysis. These samples were then stored at 4°C at the Scion Campus in Rotorua before analysis.

Figure 2.14. Modified stainless steel soil hoffer taking a 0 - 10cm soil sample. (Photo of Loretta Garrett, by Michelle Harnett).

2.3.6.4.1 Sample preparation and laboratory analysis

Chemical analyses of soil samples were used to estimate the fertility of each plot. Soil samples were dried in aluminium containers at 40°C. The dried samples were passed through a 2 mm sieve to remove leaf litter and additional detritus while the < 2 mm portion of soil was retained for analysis (Figure 2.15). The sieved samples were put in plastic pottles and sent to Veritec Laboratory, Rotorua for soil chemistry analyses.

Figure 2.15. Soil sieving. (Photo by Loretta Garrett).

The following methods were used by Veritec to extract soil chemical properties from the samples. Total carbon and total nitrogen were analysed by a LECO CNS analyser using the modified Dumas technique. The pH was measured using 1:2:5 soil/water suspension. Bray phosphorus was measured by Flow Injection Analysis (FIA) colorimetry after sequential 1:10 Bray 2 (NH_4F/HCI) Extraction. The remaining elements of Aluminium (Al), boron (B), Calcium (Ca), Copper (Cu), Iron

(Fe), Magnesium (Mg), Manganese (Mn), Sodium (Na), Phosphorus (P), Potassium (K) and Zinc (Zn) were measured by ICP-MS after Mehlich 3 extraction.

2.3.7 Statistical Analysis

The data were plotted by site to identify any outliers. Irregularities in the data were checked against the original data sources and corrected where necessary. Trees with a stem diameter of < 10 cm at breast height were excluded from the analysis to prevent young self-established individuals skewing the merchantable stems information. Site 15 was not altered due to the young age of the site.

2.3.7.1 Height/Diameter

As height measurements were only taken from a representative sample of trees within each PSP, regression equations (Equation 2-1) were used to estimate all tree heights which were required to predict volume as an estimate for site productivity. Height versus stem diameter graphs for each PSP were fitted with non-linear regression curves. The regression equations from these curves were used to estimate all tree heights within the PSPs for each site. Mean heights for each PSP were obtained from these height estimates.

$$H = \alpha D^b \tag{2-1}$$

where D is stem diameter (cm), a is a constant and b is the power specific to each PSP.

The quadratic mean diameter (D_q) (cm) was used as a measure of mean stem diameter as it is conventionally used in forestry. The quadratic mean diameter is regarded as a more accurate measurement of stem diameter than the arithmetic mean (DBH) (Curtis & Marshall, 2000). The D_q was calculated using the equation from Curtis and Marshall (2000).

$$D_q = \sqrt{\frac{(\sum D^2)}{n}} \tag{2-2}$$

where D is stem diameter (cm) of individual trees and n is the total number of trees.

2.3.7.2 Stand mortality

Reineke's stand density index (SDI) was used to estimate self-thinning across three relative stand densities (100%, 55% and 35%) (Reineke, 1933). The SDI approach is based on the size-density relationship between stand density (stems ha^{-1}) and quadratic mean diameter (Dq) (Drew & Flewelling, 1977, 1979; Long, 1985; VanderSchaaf, 2013). The maximum stand density for tōtara was estimated using Yoda's -3/2 power law of self-thinning to estimate the maximum mean tree size attainable for any stand density (Drew & Flewelling, 1977, 1979). The SDI approach is used in forestry as a theoretical reference to identify levels of intra-specific competition and mortality to inform density management as it is independent of site fertility and stand age (Drew & Flewelling, 1977, 1979; Long, 1985; VanderSchaaf, 2013). The maximum stand density for all tōtara sites was set to 1700 stems ha^{-1} with a D_q of 30 cm. SDI was calculated using a modified equation from VanderSchaaf (2013):

$$SDI = N(D_q/30)^b \quad (2\text{-}3)$$

where N is stems per hectare, D_q is quadratic mean diameter (cm) and b is the exponent of Reineke's equation which is equal to 1.605.

2.3.7.3 Age

The ages of all planted stands were known and were obtained from their corresponding databases. The majority of the naturally regenerated stands had previous age information available from studies by Bergin and Kimberley (2012) and McKinley and Steward (2016) who took wood increment core samples from the stands. The ages of the remaining sites were assumed based on the PSPs average stem diameter. For analysis, the age of all the tōtara trees at each site were considered to be the same.

2.3.7.4 Basal Area and Volume

Individual tree basal area (g) (m^2) was calculated using the following equation:

$$g = \frac{\pi(D/2)^2}{1000000} \quad (2\text{-}4)$$

where π is 3.14 and *D* is stem diameter (mm). Total basal area (G) ($m^2\ ha^{-1}$) was calculated as the sum per hectare of the cross-sectional stem area at DBH (1.4 m) for all individual trees within the PSP.

The merchantable volume (*V*) of each tōtara tree was calculated using the following equations from Beets *et al.* (2012), Ellis (1979), Richardson *et al.* (2009) and Todoroki and Steward (2019). The four volume equations were compared against two tōtara specific datasets to identify which equation provided the most appropriate fit to the data. The datasets used for this comparison was the independent dataset from Steward and McKinley (2019) and the dataset collected from this study. The equation from Beets *et al.* (2012) calculated the volume of each tree as:

$$V = (aX^b) \tag{2-5}$$

where *X* is stem diameter squared (cm^2) multiplied by Height (m) (D^2H), *a* is 0.0000545 and *b* is 0.968. The equation from Ellis (1979) calculated the merchantable volume of each tree as:

$$V = \alpha D^b H^c \tag{2-6}$$

where *D* is stem diameter (cm), *a* is 0.000147, *b* is 1.985, and *c* is 0.639.The following equation from Richardson *et al.* (2009) calculated the merchantable volume of each tree as:

$$V = \alpha(D^2H)^b \tag{2-7}$$

where *D* is stem diameter (cm) and *H* is height (m), *a* is 0.0000598, *b* is 0.946. The following equation from Todoroki and Steward (2019) calculated the merchantable volume as:

$$V = \left(a + bD_{(0.3)}^2 + cH^2 + dD_{(0.3)}^2H\right) \tag{2-8}$$

where $D_{(0.3)}$ is stem diameter (cm) estimated at a stump height of 0.3 metres, *H* is height (m), *a* is 0.000689, *b* is -0.0000377, *c* is -0.00000246 and *d* is 0.0000391.

The total volume per hectare in each PSP was calculated as the sum per hectare of volume for all individual trees. Volume mean annual increment (MAI) ($m^3\ h^{-1}\ y^{-1}$) in each PSP was calculated by dividing the total volume per hectare at each site by age.

2.3.7.5 Biomass

There is little above-ground biomass information available for tōtara from the literature, as a result there are no species specific biomass equations for stem biomass or carbon (Höck *et al.*, 2017). An independent dataset obtained from a study by Steward and McKinley (2019) was used to identify the most appropriate equation to calculate the biomass of the inventoried volume of tōtara for each site. The study examined the wood density of tōtara across representative sites around New Zealand. Eight sites relevant to the current calibration dataset were selected and were separated into two groups based on their age; young sites < 65 years old and mature sites > 65 years old. Density values for wood (ρ) were obtained from the study (Table 2.3) (Steward & McKinley, 2019).

Table 2.3. Summary of the eight tōtara stands examined by Steward and McKinley (2019). Data were separated based on age; young sites < 65 years old and mature sites ≥ 65 years old. Heights were estimated for each stand using Equation 2-1. Mean ± standard error.

Stand	Age	No. trees	DBH (cm)	Height (m)	Wood density (kg m^{-3})
Glenbervie	63	30	35.60 ± 1.51	10.64 ± 0.05	443 ± 5.66
Holt	52	30	27.72 ± 0.53	12.35 ± 0.08	424 ± 4.89
Kaingaroa	53	40	27.30 ± 0.66	11.67 ± 0.11	397 ± 4.13
Mamaku	57	30	28.20 ± 1.06	10.52 ± 0.33	436 ± 5.08
Tapapakanga	14	418	9.60 ± 0.12	5.84 ± 0.01	448 ± 1.63
Kaeo	65	28	38.45 ± 1.78	20.84 ± 0.52	432 ± 4.81
Paringahau	68	30	31.44 ± 0.82	13.27 ± 0.09	448 ± 5.29
Puhipuhi	110	45	37.30 ± 1.23	22.71 ± 0.23	453 ± 5.21

Four equations obtained from the literature were used to compare the stem biomass for tōtara $B_{(V)}$ ($m^3\ tree^{-1}$): Beets *et al.* (2012), Coomes *et al.* (2002), Ellis (1979) and Todoroki and Steward (2019). These four equations were selected as they have previously been used in the literature to estimate volume of tōtara.

The stem biomass $B_{(V)}$(m^3 $tree^{-1}$) was calculated using the following equation from Beets *et al.* (2012):

$$B_{(V)} = (aX^b)\rho \quad (2\text{-}9)$$

where a is 5.45, X is stem diameter squared (cm^2) multiplied by Height (m) (D^2H), b is 0.968 and ρ is the species-specific wood density (kg m^{-3}). The equation from Coomes *et al.* (2002) calculated $B_{(V)}$ as:

$$B_{(V)} = \alpha\rho(D^2H)^b \quad (2\text{-}10)$$

where a is 0.0000598, D is stem diameter (cm), H is height, b is 0.946 and ρ is the species-specific wood density (kg m^{-3}). The equation from Ellis (1979) calculated $B_{(V)}$ as:

$$B_{(V)} = (\alpha D^b H^c)\rho \quad (2\text{-}11)$$

where D is stem diameter (cm), a is 0.000147, b is 1.985, c is 0.639 and ρ is the species-specific wood density (kg m^{-3}). The equation for young trees from Todoroki and Steward (2019) calculated $B_{(V)}$ as:

$$B_{(V)} = \left(a + bD_{(0.3)}^2 + cH^2 + dD_{(0.3)}^2 H\right)\rho \quad (2\text{-}12)$$

where $D_{(0.3)}$ is stem diameter (cm) estimated at a stump height of 0.3 metres, H is height, a is 0.000689, b is -0.0000377, c is -0.00000246, d is 0.0000391 and ρ is the species-specific wood density (kg m^{-3}). The equation for mature trees from Todoroki and Steward (2019) calculated $B_{(V)}$ as:

$$B_{(V)} = (aD_{(0.3)}^b H^c)\rho \quad (2\text{-}13)$$

where $D_{(0.3)}$ is stem diameter (cm) estimated at a stump height of 0.3 metres, H is height, a is 0.0000484, b is 2, c is 0.944 and ρ is the species-specific wood density (kg m^{-3}).

The equation selected as the most appropriate fit to the independent dataset was then used to estimate $B_{(V)}$ of the fifteen sites use in this study. The mean wood density $\rho = 443$ kg m^{-3} was obtained from Steward and McKinley (2019) full dataset (Table 2.3).

The biomass of carbon above ground per tree, $B_{(cag)}$ (kg $tree^{-1}$) was calculated using a modified version of Beets *et al.* (2012) equation for carbon. This was calculated by multiplying V by ρ. The allometric equations for mixed species were used to calculate the mass of branches < 10 cm in diameter and foliage which were then added to the $B_{(cag)}$ equation:

$$B_{(cag)} = 0.5(0.905\rho V + 0.0175D^{2.20} + 0.0171D^{1.75}) \quad (2\text{-}14)$$

where D is stem diameter (cm), ρ is the species-specific wood density (kg m^{-3}) and V is volume m^3 $tree^{-1}$. The ratio estimator of 0.905 was used as an adjustment factor to convert the ρ to mean density for the entire tree above ground (Beets *et al.*, 2012). The equation was multiplied by 0.5 as it is assumed 50% of tree biomass is carbon (Beets *et al.*, 2012; Williams & Norton, 2012). The biomass of carbon for each tree was then summed for each PSP and divided by the size of the plot. Carbon biomass was then converted from kg ha^{-1} to t ha^{-1}.

2.3.7.6 Statistical Analysis

Statistical analyses were undertaken using the REG Procedure of SAS Version 9.4 (SAS Institute, 2015). The multiple linear regression backward elimination analysis was used to identify the key variables which contributed to the growth of tōtara in terms of volume mean annual increment (m^3 ha^{-1} yr^{-1}). The variables analysed in the backwards elimination regression are shown in Table 2.4. The multiple linear regression backward elimination analysis procedure started with all 22 independent variables in the model. The model then removed variables of least significance, one

by one, in order of those that contributed the least explanatory value (R^2) to the model and had the F statistic p-value greater than 0.1. The model continued automatic iterations removing variables until the selected criteria level was met, without a statistically insignificant loss of model fit. The backwards elimination method has some weaknesses, including the tendency of keeping more variables and a higher Mallow's C(p) criteria value than other methods (Beale, 1970; Dunkler *et al.*, 2014). Despite these weaknesses, this method is not better or worse than the other multiple regression variable selection methods such as forward selection or stepwise selection (Murtaugh, 2009). Indeed, some methods are more applicable under certain circumstances, depending on the nature of the problem and the availability of data (Haque *et al.*, 2018). The backwards elimination method was chosen for variable selection for the multiple linear regression analysis as the preliminary statistical analysis found that forward selection or stepwise selection methods were unsuitable for this dataset. Soil texture information were retrieved from Landcare Research (Appendix A, Table 2.7). The data were obtained from Landcare Research's New Zealand Fundamental Soil Layer (FSL) textural classification map with a 100 m resolution (Meason *et al.*, 2011). Climate data for each site was retrieved from the Virtual Climate Stations Network (VCSN). Mehlich 3 aluminium, iron and sodium were excluded from the analysis as they are not readily available for plant uptake. Sites which had no soil chemistry information were not included in the analysis, therefore, the three plots from Site 15 and the four plots from Site 8 were excluded from the SAS analysis.

Table 2.4. Independent variables used in the backward elimination multiple regression to predict productivity of tōtara. HCP: horizontal coplanar; PRP: perpendicular coplanar; Min: minimum; Max: maximum; Bray P: bray phosphorus; Mehlich 3 extracted nutrients; B: boron; Mg: magnesium; P: phosphorus; K: potassium; Ca: calcium; Mn: manganese; Cu: copper; Zn: zinc.

Elevation	Latitude	Total Carbon	Soil Texture
Rainfall	Mean Temperature	Total Nitrogen	Region
HCP	Max Temperature	Total Phosphorus	Mehlich 3 (B, Mg, P,
PRP	Min Temperature	Bray P	K, Ca, Mn, Cu & Zn)

2.4 Results

2.4.1 Estimated Heights

The heights of all tōtara trees within each plot were estimated by fitting non-linear regression curves to graphs with measured height and stem diameter (cm) results (Figure 2.16). Following this, a power regression equation was fitted to the data and was subsequently used to estimate the heights of all tōtara trees within each plot for the fifteen sites (Figure 2.16).

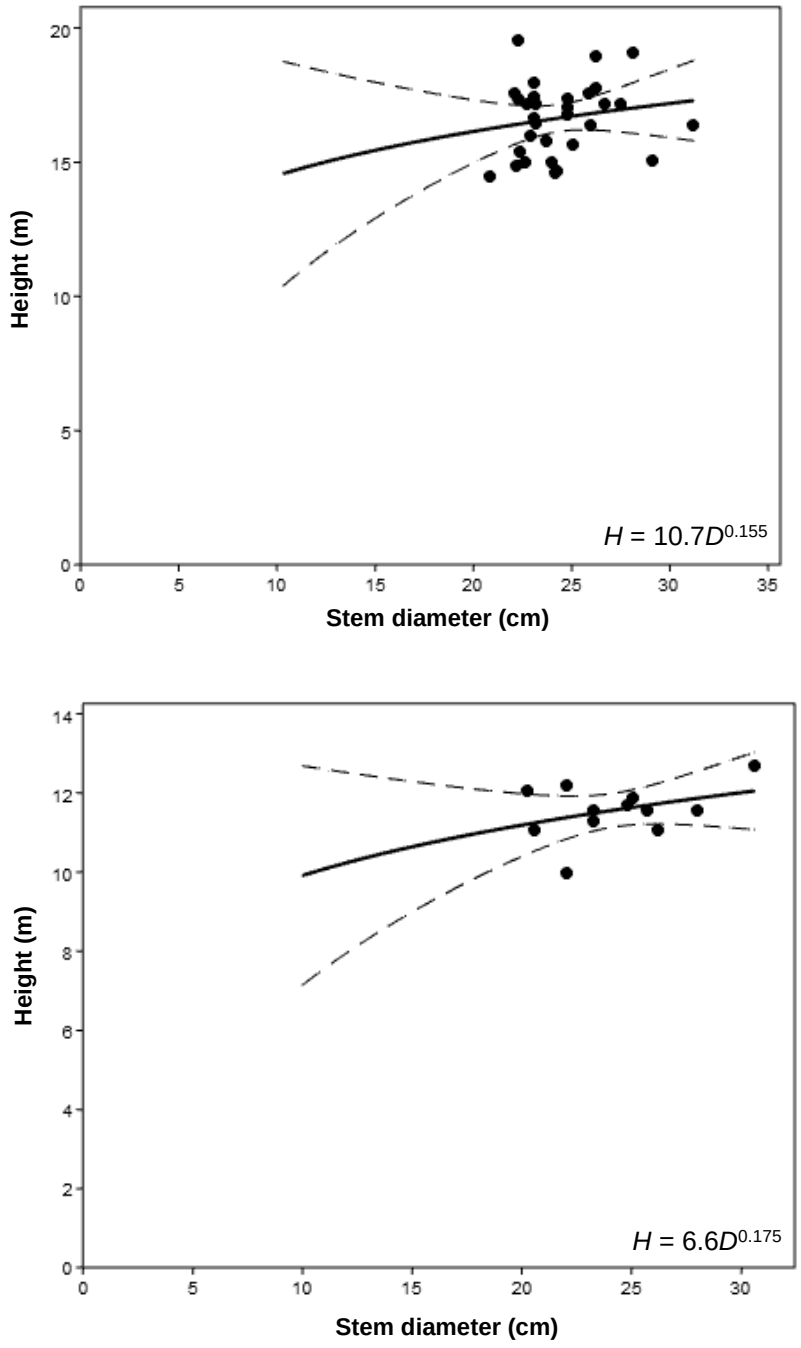


Figure 2.16. a & b. Non-linear relationship between height (m) and stem diameter (cm) with 95% confidence bands (dashed lines) for all tōtara trees at Site 13 (top) and Site 14 (bottom) based on Equation 2-1. These are examples of those used to estimate heights of all tōtara trees in each plot, at each study site.

The relationship between measured heights and regression estimated heights had a strong linear relationship with an $R^2 = 0.93$ (Figure 2.17). This relationship was found to be highly significant ($p < 0.01$). The heights ranged from 1.5 m to 28 m across all sites, with the majority of heights between 10 m to 18 m (Figure 2.17). The height model was strongest at estimating heights of trees < 5 m (Figure 2.17). There was more variation in the model at heights ≥ 20 m (Figure 2.17).

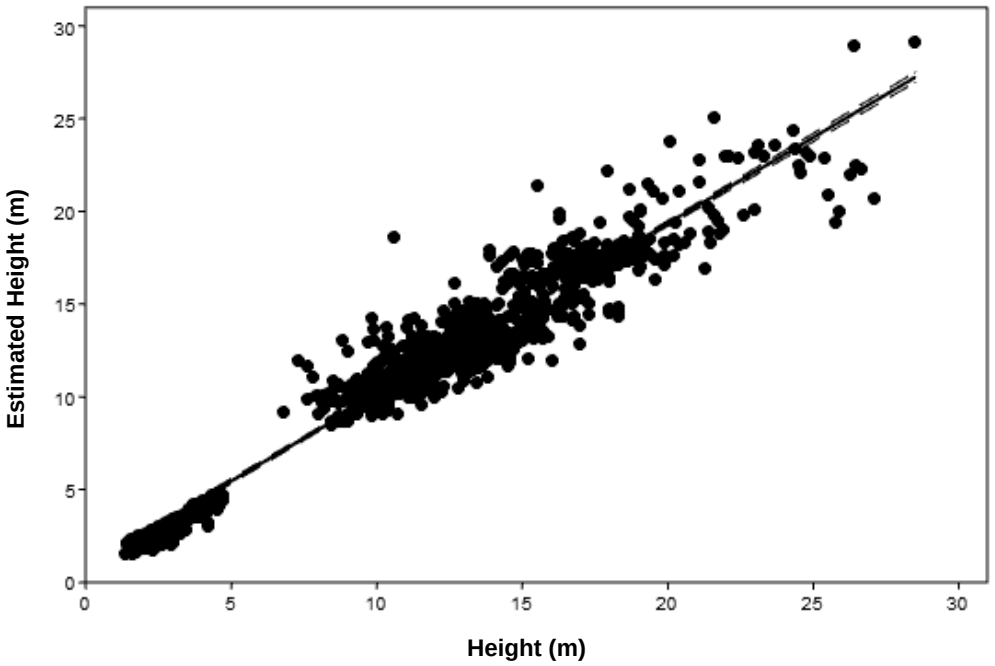


Figure 2.17. Relationship between estimated height (m) and measured height (m) of all tōtara trees from the fifteen study sites ($R^2 = 0.93$).

Across all sites there was a moderate correlation between estimated height (m) and stem diameter (cm) with an $R^2 = 0.65$ (Figure 2.18). Tree height ranged from < 2 m to 30 m across stem diameters from < 1 cm to 130 cm (Figure 2.18). Most trees from the dataset had stem diameters between 10 cm and 50 cm, with corresponding heights between 10 m and 20 m (Figure 2.18). This relationship is potentially affected by stand density and site fertility (Figure 2.18).

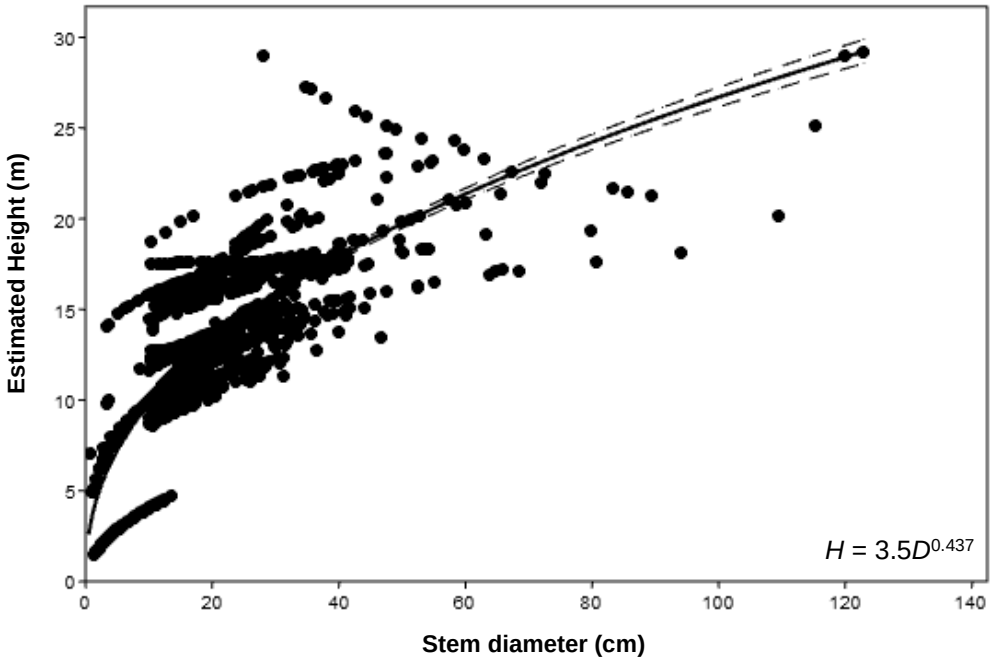


Figure 2.18. Non-linear relationship between estimated height (m) and stem diameter (cm) with 95% confidence bands (dashed lines) for all tōtara trees from the fifteen study sites ($R^2 = 0.65$).

2.4.2 Volume

The mean stand volume of tōtara for the fifteen study sites ranged from 0.74 $m^3 ha^{-1}$ to ≥ 2458 $m^3 ha^{-1}$ (Figure 2.19). The volume equation from Richardson *et al.* (2009) gave a higher estimate of mean stand volume across all sites when compared to the equation from Ellis (1979) (Figure 2.19). The equation from Beets *et al.* (2012) and Todoroki and Steward (2019) gave a lower estimate of mean stand volume compared to the equation from Ellis (1979) (Figure 2.19). Site 6 and Site 10 had mean stand volumes ≥ 900 $m^3 ha^{-1}$, compared to the other sites which had volumes < 900 $m^3 ha^{-1}$ (Figure 2.19). The smallest mean stand volume was at Sites 1, 4, 9, 11 and 15 with < 180 $m^3 ha^{-1}$ (Figure 2.19). The largest mean stand volume was in Site 6 with 1431 $m^3 ha^{-1}$ (Figure 2.19). The volumes estimated by Beets *et al.* (2012) and Todoroki and Steward (2019) were not significantly different (Figure 2.19).

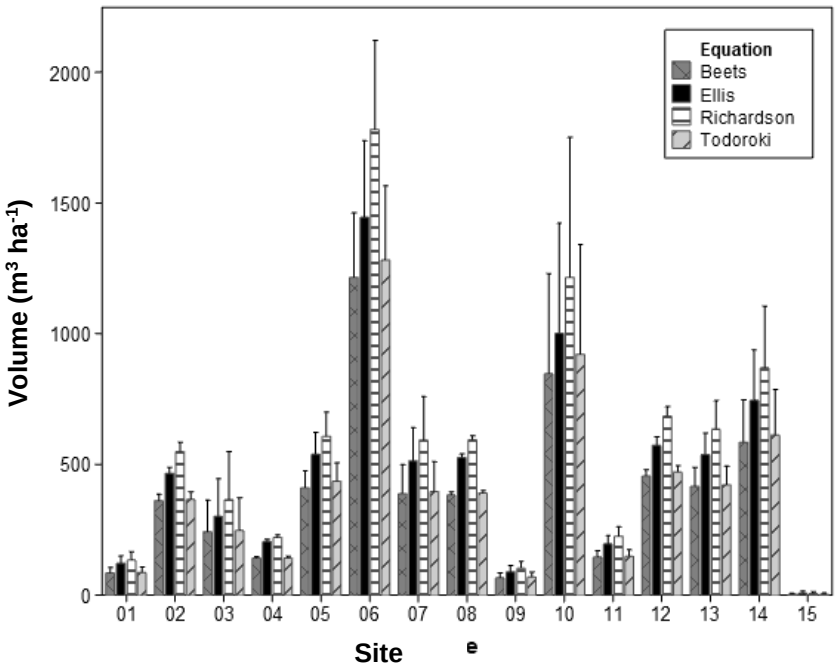


Figure 2.19. Mean stand volume (m^3 ha^{-1}) with standard errors for tōtara across the fifteen study sites using the four volume equations (Equations 2-5, 2-6, 2-7 & 2-8) obtained from the literature.

2.4.3 Biomass

The four volume equations were tested against the independent dataset from Steward and McKinley (2019) to compare estimates of stem biomass (Figure 2.20). Across the young tōtara sites, the equations from Beets *et al.* (2012) provided high estimates of stem biomass similar to Ellis (1979) (Figure 2.20). The equations from Coomes *et al.* (2002) and Todoroki and Steward (2019) provided lower estimates of stem biomass compared to Ellis (1979) (Figure 2.20). The equations from Todoroki and Steward (2019) and Coomes *et al.* (2002) provided the best fit to this young dataset (Figure 2.20).

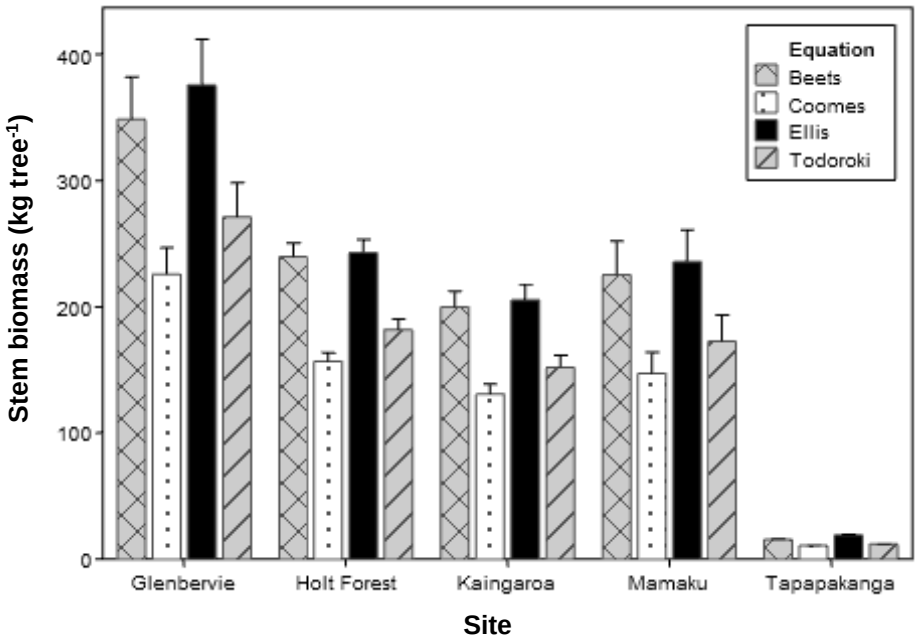


Figure 2.20. Mean stem biomass (kg tree^{-1}) with standard errors for young tōtara < 65 years at five study sites using the four modified volume equations (Equations 2-9, 2-10, 2-11, & 2-12) obtained from the literature.

The mean stem biomass at the three mature tōtara sites ranged from 220 kg tree^{-1} to 810 kg tree^{-1} (Figure 2.21). The equation from Coomes *et al.* (2002) and Todoroki and Steward (2019) provided lower estimates of stem biomass compared to Ellis (1979) (Figure 2.21). The equation from Beets *et al.* (2012) provided higher estimates of stem biomass compared to Ellis (1979) (Figure 2.21).

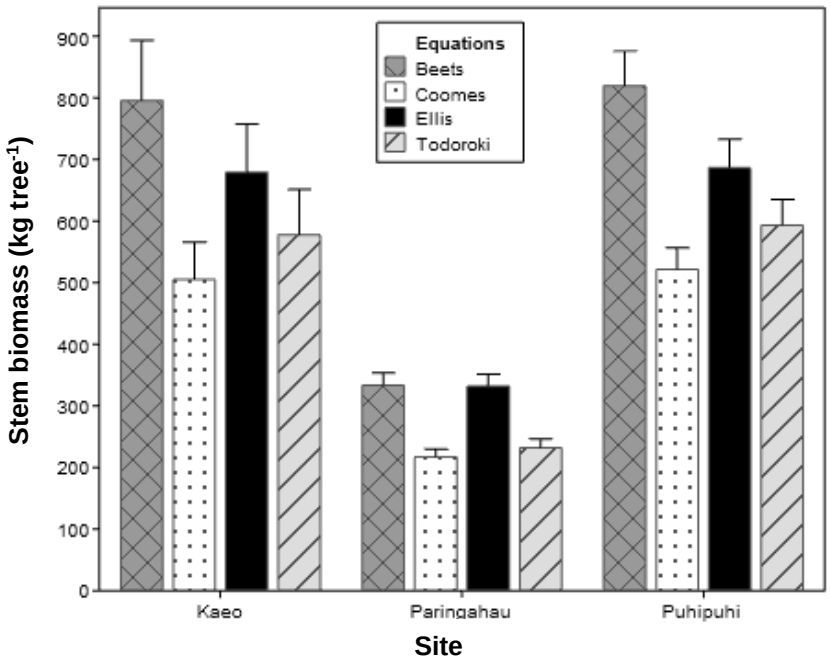


Figure 2.21. Mean stem biomass (kg tree^{-1}) with standard errors for mature tōtara ≥ 65 years at three study sites using the four modified volume equations (Equations 2-9, 2-10, 2-11 & 2-13) obtained from the literature.

Overall, the equation from Todoroki and Steward (2019) was selected as the most appropriate estimate of stem biomass (Figure 2.20 & Figure 2.21). The equation was developed from a tōtara dataset specifically for the species and provided the median estimates between the four equations (Figure 2.19, Figure 2.20 & Figure 2.21). This equation was selected to compare the mean stand biomass and carbon biomass across the fifteen study sites used in this study (Figure 2.22 & Figure 2.23).

The largest mean stem biomass was at Site 6 with 568 t ha^{-1} (Figure 2.22). Sites 1, 4, 9 and Site 15 had stem biomass < 65 t ha^{-1} (Figure 2.22). The smallest stem biomass was at Site 15 with 2.8 t ha^{-1} (Figure 2.22). The stem biomass at Site 10 and Site 14 were > 200 t ha^{-1} (Figure 2.22). The mean stem biomass of tōtara for all sites was 173.3 t ha^{-1} (Figure 2.22).

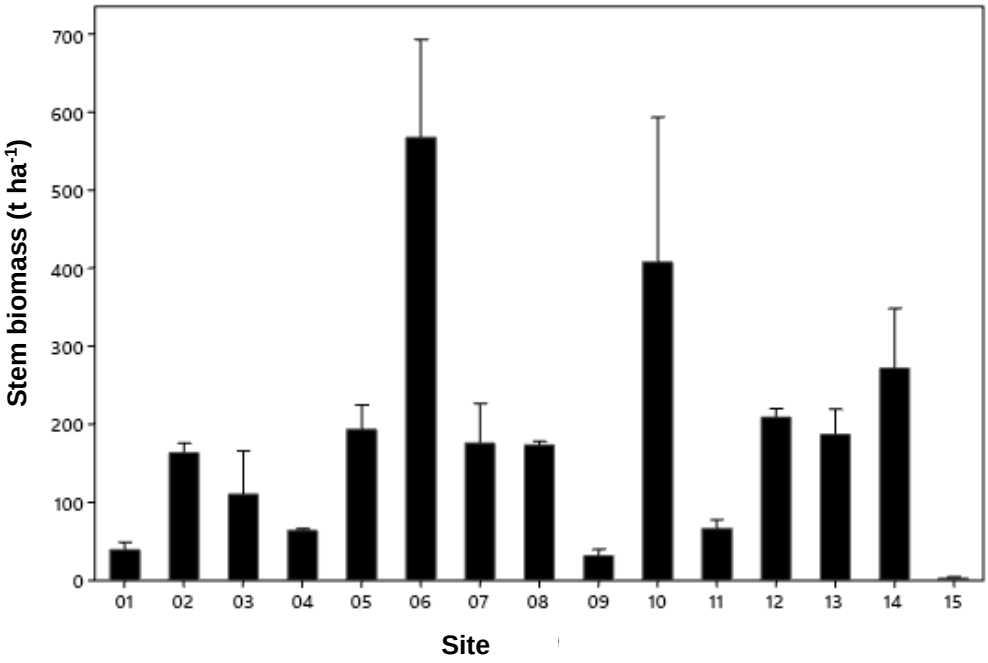


Figure 2.22. Mean stem biomass (t ha^{-1}) with standard errors for the fifteen study sites based on Equation 2-12 & Equation 2-13.

The mean biomass of carbon above ground for all sites was 90.8 t ha^{-1} (Figure 2.23). The largest carbon biomass was at Site 6 with 290 t ha^{-1} (Figure 2.23). Site 15 had the lowest carbon biomass 1.8 t ha^{-1} (Figure 2.23). The carbon biomass at Site 10 and Site 14 were ≥ 113 t ha^{-1} (Figure 2.23).

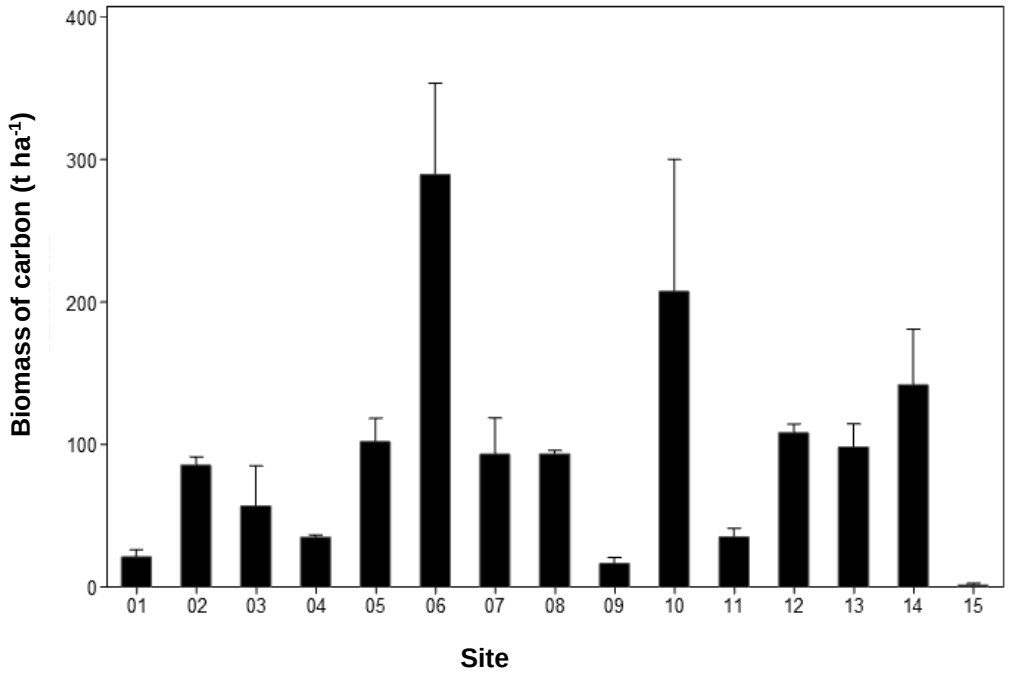


Figure 2.23. Mean biomass of carbon above ground (t ha^{-1}) with standard errors for the fifteen study sites, based on Equation 2-14.

The sites with the highest stem biomass and carbon biomass were Sites 6, 10 and Site 14 (Figure 2.22 & Figure 2.23). The sites with the lowest stem biomass and carbon biomass were Sites 1, 4, 9, 11 and Site 15 (Figure 2.22 & Figure 2.23). Age, stand density and site fertility are potential factors affecting the productivity of these sites (Figure 2.19, Figure 2.22 & Figure 2.23).

2.4.4 Stand mortality

The relationship between stand density (stems ha^{-1}) and quadratic mean diameter (cm) showed mortality occurred across sites as the trees increased in quadratic mean diameter, and the stand density of the plots decreased (Figure 2.24). Site 8 had a high stand density as the trees were ≤ 20 cm in diameter, and stand densities were ≥ 2800 stems ha^{-1} (Figure 2.24). As the quadratic mean diameter increased to > 30 cm, the stand density with trees of that size decreased to ≤ 1200 stems ha^{-1} (Figure 2.24). Plots from Sites 6, 10 and 14 had diameters ≥ 40 cm and stand densities ≤ 500 stems ha^{-1} (Figure 2.24).

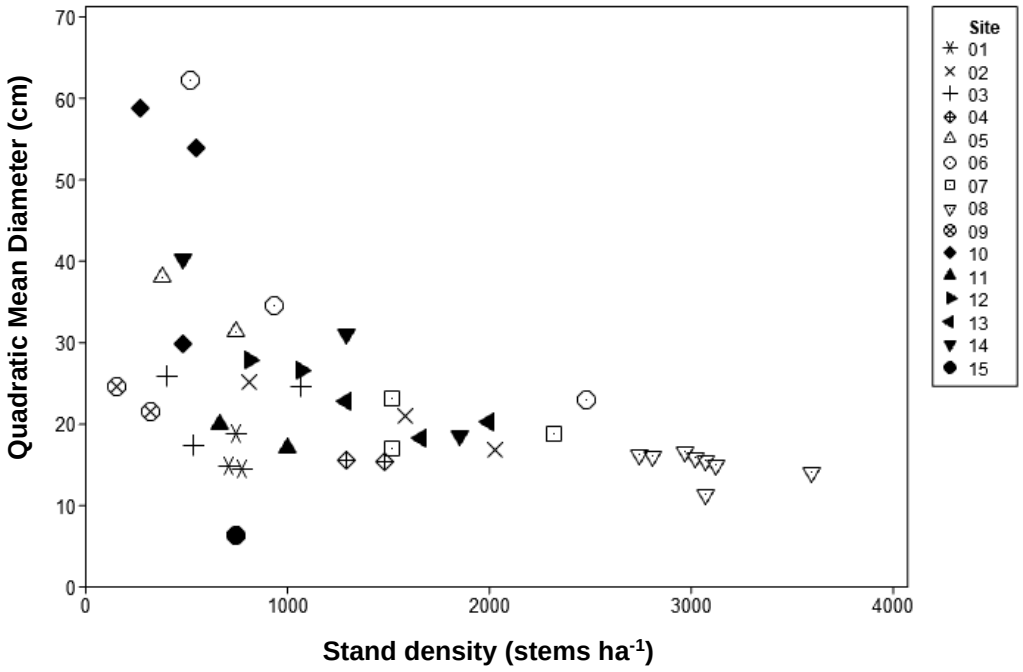


Figure 2.24. Relationship between quadratic mean diameter (cm) and stand density (stems ha^{-1}) across the fifteen study sites.

The log relationship between quadratic mean diameter and stand density provided an indication of the potential optimal and maximum stand densities for tōtara (Figure 2.25). The maximum stand density represents the highest stand density at a given quadratic mean diameter that can exist for tōtara across sites. Stand density ranged from 156 stems ha^{-1} to 3073 stems ha^{-1} (Figure 2.25). The SDI model indicated maximum stand density is at the 100% relative density line as no plots had stand densities above this line (Figure 2.25). The most densely stocked plot close to the maximum self-thinning line was at Site 6 with a stand density of 2484 stems ha^{-1} and D_q of 21 cm (Figure 2.24 & Figure 2.25). In theory, mortality is more likely to occur due to higher intra-specific competition between the 55% and 100% relative density lines. The self-thinning model indicates the plots below the 35% relative density line were potentially under-stocked (Figure 2.25). This suggests that the plots below this line have little intra-specific competition and growth is likely to continue to reasonable stem sizes ≥ 30 cm compared to sites with higher stocking. Therefore, there would be little need for silvicultural management of these understocked stands. The majority of plots were at stand densities between the 35% line and 75% relative stand density (Figure 2.25). The theoretical optimal stocking of the SDI for tōtara is suggested to be between the 35% understocked and 75%

fully stocked stands, therefore the plots around the 55% relative stand density line are likely to have optimal stocking for silviculture.

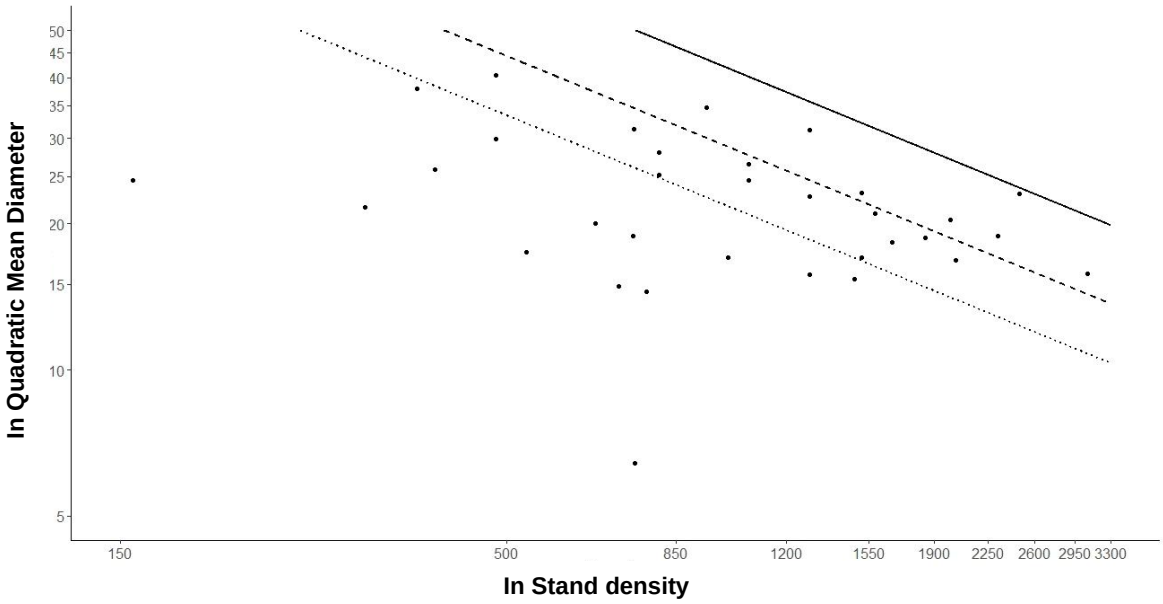


Figure 2.25. Log relationship between quadratic mean diameter and stand density with fitted self-thinning lines at three relative stand densities (35%, 55%, 100%), based on Equation 2-3. Solid black line represents maximum relative density at 100% (—), solid dashed black line represents optimal stand density at 55% (- - -) and small dotted line represents the relative stand density at 35% (⋯⋯).

2.4.5 Stand productivity

The relationship between mean stand volume ($m^3\ ha^{-1}$) and mean stand basal area ($m^2\ ha^{-1}$) was highly correlated with an $R^2 = 0.90$ (Figure 2.26). The positive linear relationship suggests that as stand volume increases, there is a steady increase in basal area. There is no plateau identified in the regression indicating that the maximum capacity for stand basal area has not been reached. The majority of sites had basal areas < 80 $m^2\ ha^{-1}$ and there were only two sites with basal areas > 120 $m^2\ ha^{-1}$, which were older sites (Site 6 & Site 10) (Figure 2.26). Given that there were only two sites with basal areas > 120 $m^2\ ha^{-1}$ more data is needed to confirm this relationship.

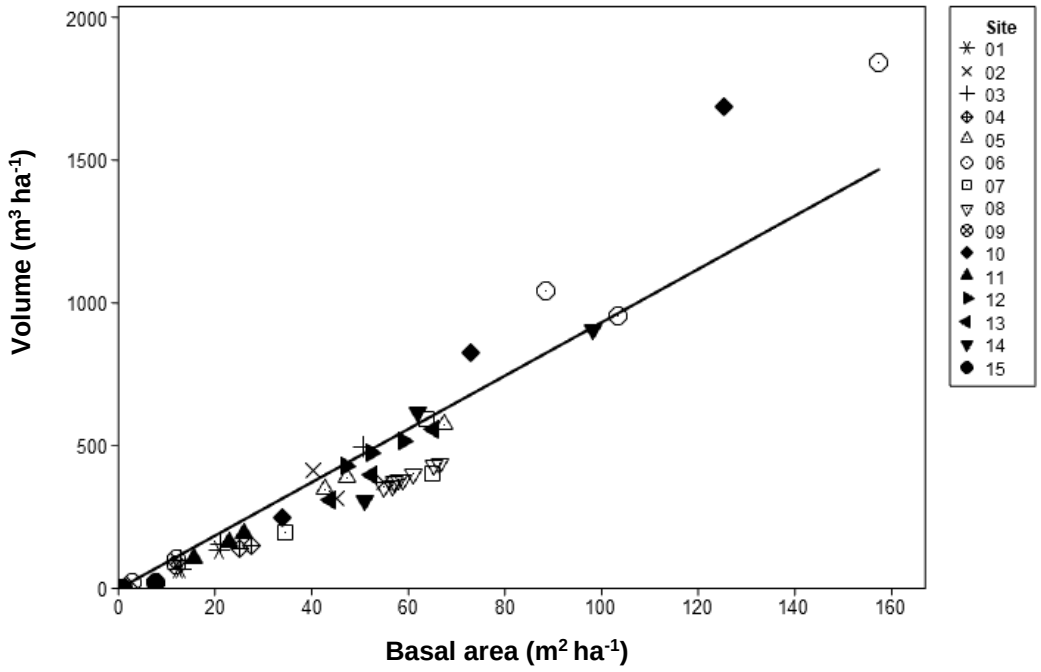


Figure 2.26. Relationship between mean stand volume (m^3 ha^{-1}) and mean basal area (m^2 ha^{-1}) (R^2 = 0.90).

There was no relationship between volume MAI (m^3 ha^{-1} yr^{-1}) and HCP EC_a (mS m^{-1}) across sites ($p > 0.05$) (R^2 = 0.02) (Figure 2.27). There was a large variation of HCP EC_a across all sites (Figure 2.27). An outlier from Site 15 was removed from this analysis as the HCP EC_a value from the plot was > 500 mS m^{-1} (Figure 2.27). Plots from Site 10, 12 and one plot from Site 14 had high HCP EC_a values > 200 mS m^{-1} (Figure 2.27). A large portion of plots had HCP EC_a values < 100 mS m^{-1} (Figure 2.27).

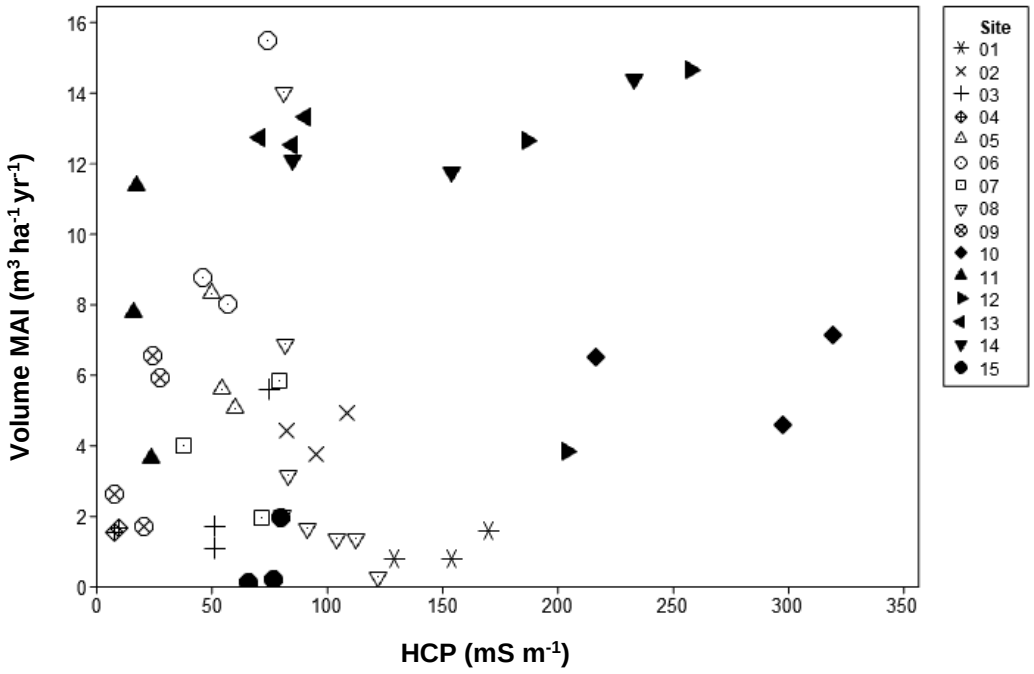


Figure 2.27. Relationship between volume mean annual increment (MAI) ($m^3\,ha^{-1}\,yr^{-1}$) and HCP ECa ($mS\,m^{-1}$) (horizontal coplanar receiver, apparent electromagnetic conductivity) with an outlier from Site 15 removed ($R^2 = 0.02$).

No significant relationship was found between volume MAI ($m^3\,ha^{-1}\,yr^{-1}$) and PRP EC_a ($mS\,m^{-1}$) across sites ($p > 0.05$) ($R^2 = 0.01$) (Figure 2.28). There was a large range of PRP EC_a between sites which ranged from < 10 $mS\,m^{-1}$ to 135 $mS\,m^{-1}$ (Figure 2.28).

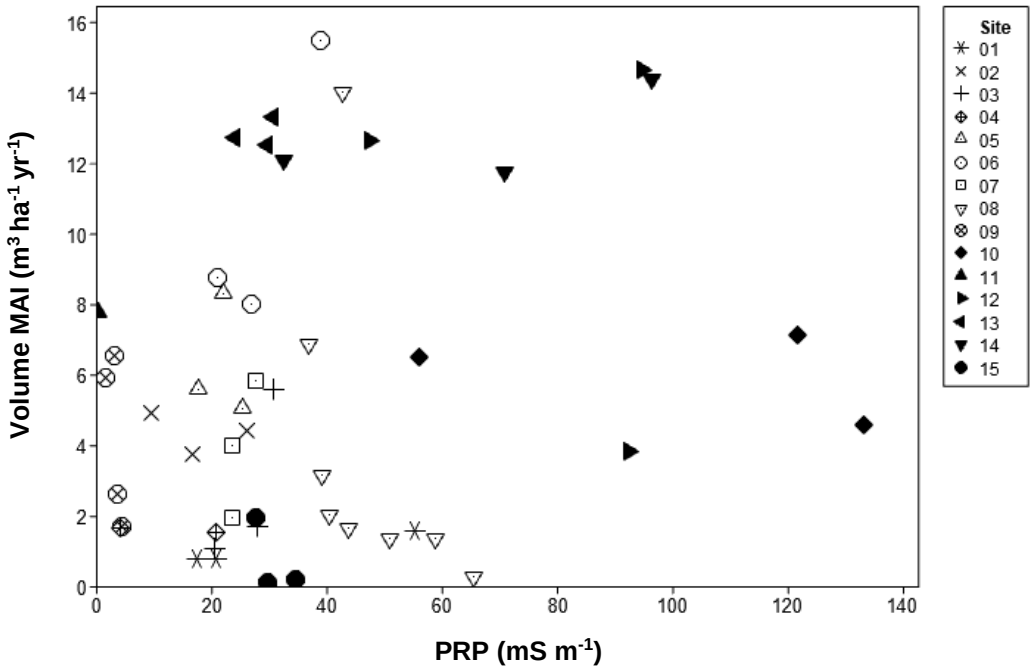


Figure 2.28. Relationship between volume mean annual increment (MAI) ($m^3 ha^{-1} yr^{-1}$) and PRP ECa ($mS\ m^{-1}$) (perpendicular coplanar receiver, apparent electromagnetic conductivity) with outlier from Site 15 removed ($R^2 = 0.01$).

There was a moderate relationship between canopy leaf area index (LAI) ($m^2\ m^{-2}$) and basal area ($m^2\ ha^{-1}$) with an $R^2 = 0.15$ (Figure 2.29). The LAI for all stands ranged from 3 to 10 (Figure 2.29). A large portion of sites had an LAI ≥ 6 with a range of mean stand basal areas (Figure 2.29). The linear increase between LAI and basal area suggests that the maximum capacity for stand basal area has not been reached, as there is no plateau in the regression. It appears from this relationship that tōtara sites with basal areas < 100 $m^2\ ha^{-1}$ could reach LAI > 8. Given that there were only two sites with basal areas > 100 $m^2\ ha^{-1}$ more data is needed to confirm this relationship.

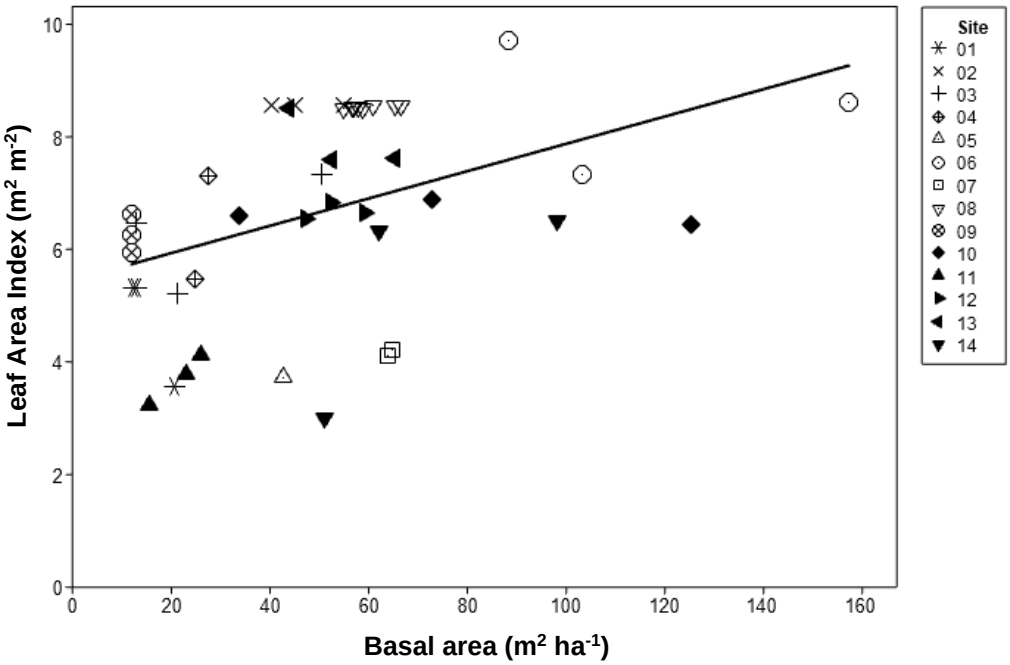


Figure 2.29. Relationship between canopy leaf area index (LAI) (m^2 m^{-2}) and basal area (m^2 ha^{-1}) ($R^2 = 0.15$).

No relationship was found between volume MAI (m^3 ha^{-1} yr^{-1}) and total nitrogen (%) ($p > 0.05$) ($R^2 = 0$) (Figure 2.30). Total nitrogen ranged from 0.20% to 0.65% (Figure 2.30). All sites showed small variations in total nitrogen concentrations between plots (Figure 2.30). Plots from Site 4, 6 and Site 13 had higher concentrations of total nitrogen compared to the other plots (Figure 2.30).

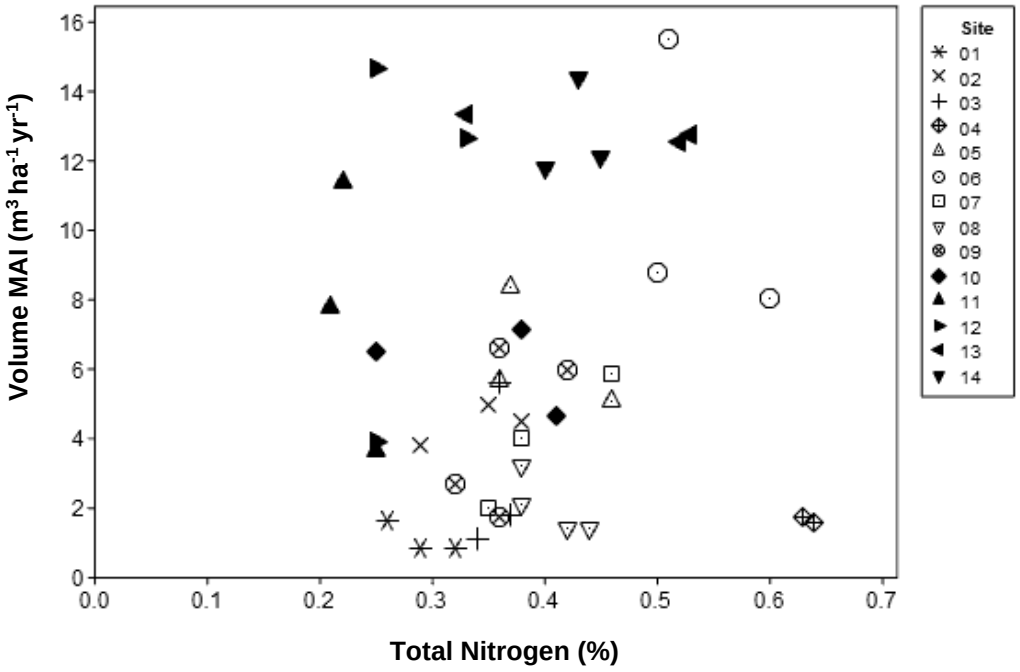


Figure 2.30. Relationship between volume mean annual increment (MAI) ($m^3\,ha^{-1}\,yr^{-1}$) and total nitrogen (%) ($R^2 = 0$).

The relationship between volume MAI and total bray P ($mg^{-1}\,kg^{-1}$) and was weakly correlated ($R^2 = 0.06$) (Figure 2.31). Total bray P varied greatly across sites (Figure 2.31). Plots from Site 6, 8, 10, 13 and Site 14 had high concentrations of bray P ≥ 60 $mg^{-1}\,kg^{-1}$ (Figure 2.31).

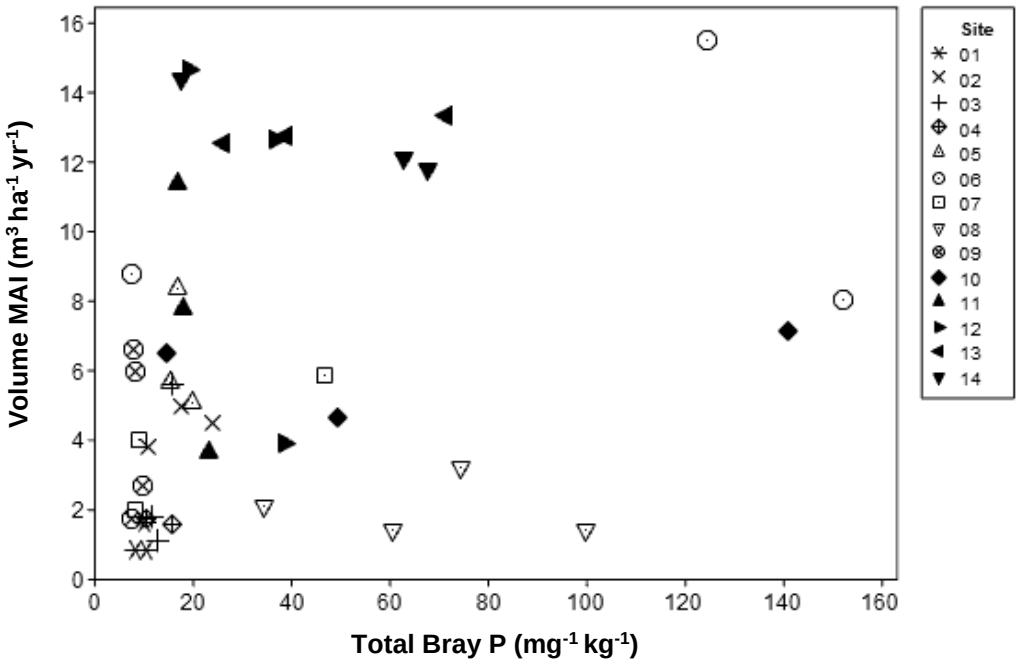


Figure 2.31. Relationship between volume mean annual increment (MAI) ($m^3\,ha^{-1}\,yr^{-1}$) and total bray P ($mg^{-1}\,kg^{-1}$) across the fourteen sites ($R^2 = 0.06$).

The relationship between volume MAI and total phosphorus (mg^{-1} kg^{-1}) was moderate with an $R^2 = 0.21$ (Figure 2.32). The majority of sites had total phosphorus concentrations between 100 mg^{-1} kg^{-1} to 220 mg^{-1} kg^{-1} (Figure 2.32). One plot from Site 6 had high concentrations of total phosphorus 300 mg^{-1} kg^{-1} and high volume MAI ≥ 15 m^3 ha^{-1} yr^{-1} (Figure 2.32). The group of plots at Sites 11, 12, 13 and Site 14 had high volume MAI ≥ 11 m^3 ha^{-1} yr^{-1} (Figure 2.32).

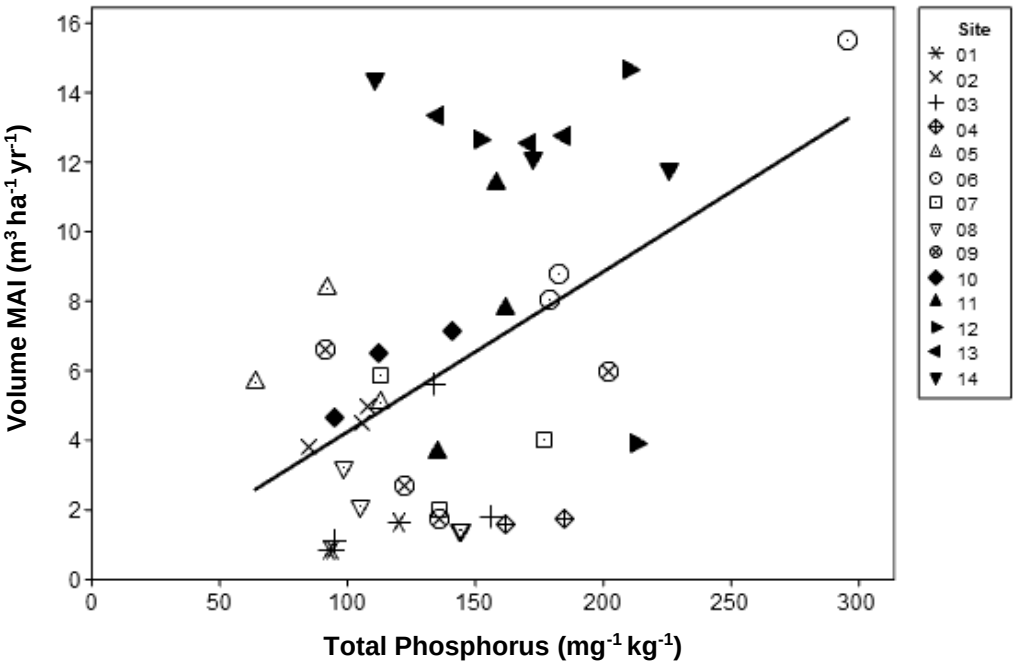


Figure 2.32. Relationship between volume mean annual increment (MAI) (m^3 ha^{-1} yr^{-1}) and total phosphorus (mg^{-1} kg^{-1}) across the fourteen sites ($R^2 = 0.21$).

2.4.6 Statistical analysis

The multiple linear regression analysis using the backward elimination method highlighted elevation, temperature (mean, max and min), rainfall, HCP, total phosphorus, Mehlich 3 magnesium, potassium, calcium and manganese as the most significant variables influencing the productivity of tōtara at a significance level of 0.1 (Table 2.5). The R^2 value of 0.95 suggested that 95% of variation of productivity could be explained by the 11 variables remaining in the model (Table 2.5). Temperature (mean, max and min) is potentially an important variable as mean, maximum and minimum temperatures were selected. Mean temperature was positively correlated with productivity (Table 2.5). This finding suggests that sites with higher mean temperatures could have higher productivity. Maximum and minimum temperatures were both significant contributors to productivity ($p \leq 0.001$)

but were negatively correlated with productivity (Table 2.5). This finding suggests that higher minimum and maximum temperatures correlate with reduced productivity. Elevation and rainfall were also negatively correlated with productivity across the study sites (Table 2.5). The edaphic drivers identified as significant for productivity were related to site fertility and soil physical properties (Table 2.5).

Table 2.5. Results of the backward elimination multiple regression analysis between the volume mean annual increment of tōtara and climatic and edaphic site variables ($R^2 = 0.95$, $C(p) = 5.09$). All variables are significant to productivity of tōtara ($p < 0.01$). Max: maximum; Min: minimum; HCP: horizontal coplanar receiver.

Variable	Parameter Estimate	Standard Error	Type II SS	F Value	Pr > F
Elevation	-0.02	0.00	24.65	17.40	0.0006
Mean Temp	2616.91	364.77	72.92	51.47	<.0001
Max Temp	-1317.75	185.43	71.55	50.50	<.0001
Min Temp	-1304.40	180.89	73.67	52.00	<.0001
Rainfall	-0.36	0.06	50.87	35.90	<.0001
HCP	-0.04	0.01	50.61	35.72	<.0001
Total Phosphorus	0.02	0.01	12.43	8.77	0.0084
Magnesium	-0.02	0.00	62.70	44.26	<.0001
Potassium	0.04	0.01	65.48	46.21	<.0001
Calcium	-0.01	0.00	50.64	35.74	<.0001
Manganese	0.01	0.00	94.08	66.40	<.0001

The regression analysis removed bray phosphorus, boron, total carbon, zinc, total nitrogen, copper, region, PRP, phosphorus, soil texture and latitude from the model as the variables were identified as not significant contributors to predicting the productivity of tōtara (Table 2.6).

Table 2.6. Variables which were removed from the backward elimination multiple regression analysis between the volume mean annual increment of tōtara and climatic and edaphic site variables. Bray P: bray phosphorus; PRP: perpendicular coplanar receiver; Mehlich P: Mehlich phosphorus.

Step	Variable Removed	Partial R-Square	Model R-Square	C(p)	F- Value	Pr > F
1	Bray P	0	0.9684	21.00	0	0.9708
2	Boron	0	0.9684	19.00	0	0.9549
3	Total Carbon	0.0001	0.9683	17.02	0.02	0.8950
4	Zinc	0	0.9683	15.02	0.01	0.9317
5	Total Nitrogen	0.0008	0.9675	13.20	0.28	0.6089
6	Copper	0.0036	0.9639	12.00	1.33	0.2712
7	Region	0.003	0.9609	10.66	1.07	0.3192
8	PRP	0.0016	0.9594	9.01	0.57	0.4634
9	Mehlich P	0.0013	0.9581	7.29	0.46	0.5072
10	Soil Texture	0.0017	0.9564	5.66	0.63	0.4374
11	Latitude	0.0065	0.9500	5.09	2.52	0.1306

2.5 Discussion

The results from this study identified key climatic and edaphic factors which influenced the productivity of tōtara stands across the North Island. The productivity of tōtara is significantly affected by regional climate drivers (Table 2.5). The significance of the mean, maximum and minimum temperatures from the multiple regression analysis suggests that the productivity of tōtara is sensitive to changes in temperature (Table 2.5). The apparent positive relationship between productivity and increasing mean temperature may explain why tōtara trees are more abundant in the northern and lowland regions of the North Island where the climate is generally warmer than that of the lower North Island and South Island (Hinds & Reid, 1957; Bergin, 2001; Simpson, 2017). Interestingly, maximum and minimum temperature were both significantly related to productivity but were negatively correlated with productivity (Table 2.5). This finding suggests that higher annual minimum and maximum temperatures correlates with reduced productivity. This may explain why tōtara trees are less abundant in regions where temperatures are too far above the optimal mean temperature (Hawkins & Sweet, 1989a; Bergin, 2000, 2001). However, it does not explain the negative correlation with minimum temperature which suggests that warmer minimum temperatures are correlated with reduced productivity. Previous studies have found that colder minimum temperatures negatively affect the growth of tōtara (Beveridge, 1962; Hawkins *et al.*, 1991; Bergin, 2000, 2001; Simpson, 2017). Therefore, further examination of the relationships among the three measures of temperature is recommended. This could identify whether the relationships could have been influenced by high collinearity between the three temperature variables, or whether the limited range of climate data may have affected these relationships.

Latitude was not selected as a significant driver of productivity, while conversely minimum, mean and maximum temperature were also included in the multiple regression model (Table 2.6). As the climatic variables of latitude and temperature are correlated, the multiple regression analysis likely removed latitude before temperature due to a) collinearity between these variables and b) latitude being a coarse indicator of temperature. The latter suggests that latitude could hide the importance of temperature and rainfall variables in predicting productivity. These variables may have localised effects in areas which were not found suitable by latitude (Austin & Van Niel, 2011; Dowling & Steward, 2018). This finding was

corroborated by an earlier study by Dowling and Steward (2018) which found latitude was a poor predictor of productivity when tōtara sites around Northland were studied using non-parametric empirical growth models. The Dowling and Steward (2018) study also identified that elevation was a good predictor of productivity and concluded that areas over 160 m above sea level (asl) had higher productivity than those at lower elevations. However, their study only focused on Northland where mean temperatures are likely to be warmer at higher elevations compared to other regions of the North Island. Elevation was found to be significantly related to productivity in our study but had a negative correlation with productivity (Table 2.5). This finding suggests that as elevation increases, the productivity of tōtara decreases. However, this may be related to the correlation between elevation and other site variables such as soil type, land-use and temperature which are more likely to drive local site productivity (Dowling & Steward, 2018). Rainfall was also identified as a significant driver for productivity (Table 2.5). The negative correlation suggests that as rainfall increases, productivity decreases. This could potentially be due to the species lack of tolerance for waterlogged soils (Hinds & Reid, 1957; Bergin, 2003a; Simpson, 2017). However, this correlation could also be affected by the limited range of rainfall across the tōtara sites in this study. Further research is recommended to explore these significant climate drivers and identify their level of contribution to the multiple regression model.

The distribution of tōtara has been described as ubiquitous as the species can grow on a range of different soil types around the country (Hinds & Reid, 1957; Hawkins & Sweet, 1989b; Bergin & Kimberley, 2003). Soil physiochemical properties were found to be significant determinants of productivity for tōtara (Table 2.5). The use of the Dualem-1 sensor provided insights into the soil physical and textural properties within each plot (Figure 2.27 & Figure 2.28). As the sites used in this study are known to not have high soil salinities, the differences in EC_a across sites were considered to be associated with soil texture and soil water holding capacity (Grisso *et al.*, 2005; Doolittle & Brevik, 2014; Gallart *et al.*, 2019). The PRP and HCP receivers both measure apparent electromagnetic conductivity but the receivers measure EC_a at different depths and receiver ranges. The PRP measures EC_a to a depth of 0.5 m with a wider range of interception (1.1 m), compared to the HCP receiver which measures EC_a to depths of 1.5 m across a narrow interception

range (1 m) (Dualem Inc, 2014). Low conductivity values ($EC_a \leq 60$ mS m^{-1}) within plots are likely to be associated with coarser textured soils, such as sand and silt, which typically have a greater soil porosity and lower soil water holding capacity (Grisso *et al.*, 2005; Gallart *et al.*, 2019). High conductivity values ($EC_a > 60$ mS m^{-1}) within plots are likely to be associated with finer textured soils, such as clay, which typically have a lower soil porosity and higher soil water holding capacity (Grisso *et al.*, 2005; Gallart *et al.*, 2019). The majority of the sites had low PRP EC_a values which indicates these sites potentially have higher sand and silt content in the soils to depths of 0.5 m (Figure 2.28) (Grisso *et al.*, 2005; Gallart *et al.*, 2019). Sites 10, 12 and 14 had high PRP EC_a values which suggests the sites are likely to have higher clay content in the soil compared to silt and sand to depths of 0.5 m (Figure 2.28) (Grisso *et al.*, 2005). The majority of the sites had medium to low HCP conductivity measurements to depths of 1.5 m ($EC_a < 100$ mS m^{-1}) (Figure 2.27). Plots from Sites 1, 8, 10, 12 & 14 had high HCP conductivity values ($EC_a >$ 100 mS m^{-1}) which suggests these plots had a higher clay content compared to silt and sand (Figure 2.27). The sites with high HCP EC_a could potentially have a higher soil water holding capacity and a greater availability of nutrients at depths between 0.5 and 1.5 m (Grisso *et al.*, 2005; Doolittle & Brevik, 2014; Gallart *et al.*, 2019). It is unknown whether these values are due to the finer textured soils or the depth of bedrock as the different topography of sites can influence the EC_a values along with metal, organic matter and branches (Grisso *et al.*, 2005; Gallart *et al.*, 2019).

It is recommended that further research should investigate a wider range of sites, across a broader range of soil types to identify whether the depth of bedrock, organic matter, effective rooting depth, soil moisture and topography may have influenced the high EC_a values. This will help identify whether the sites which had high conductivity measurements were outliers to the dataset or if more data were needed to confirm that the soil physical and textural properties were only having a minor effect on growth. Additionally, describing the soil profile down to a depth of 1.5 m would be beneficial to provide soil textural information for each site. Although costly, a series of soil chemistry analyses could be performed on the soils to a depth of 1.5 m to see what is directly influencing the soil EC_a variations at each site to provide further information as to whether effective rooting depth, porosity or available soil water could be influencing the variation in HCP and PRP. The backward elimination multiple regression analysis found HCP was significantly

related to productivity compared to PRP (Table 2.5 & Table 2.6). However, as HCP and PRP are highly correlated, the multiple regression analysis likely removed PRP before HCP due to collinearity between these variables. Interestingly, the multiple linear regression did not select soil texture in the final model. This suggests that the fundamental soil layer maps may not be a good representation of the soil textural properties at these forestry locations.

In addition to soil physical properties, the chemical properties of the soil were found to be significant for productivity (Table 2.5). Phosphorus, nitrogen and magnesium are nutrients directly involved with photosynthetic processes (Hawkins & Sweet, 1989b). Surprisingly, soil total nitrogen (%) was found to not have a significant influence on productivity (Figure 2.30 & Table 2.5). The soil total nitrogen (%) concentrations from all sites were typical of soils used for radiata pine plantation forests in New Zealand (Davis *et al.*, 2015). Therefore, the soil nitrogen concentrations between 0.2% and 0.7% across tōtara sites are likely sufficient for tōtara growth (Figure 2.30). It is not known whether nitrogen concentrations outside of this range will impede growth.

Interestingly, total phosphorus (mg^{-1} kg^{-1}) was highly significant for the productivity of tōtara ($p < 0.05$), in contrast to bray phosphorus and Mehlich 3 extracted phosphorus which were not significant ($p > 0.05$) (Figure 2.31, Figure 2.32, Table 2.5 & Table 2.6). Phosphorus is an important macronutrient required for plant growth, but the concentration range required for the growth of tōtara is not known (Watt *et al.*, 2008; Fox *et al.*, 2011). The moderate relationship between total phosphorus across sites indicated that soil phosphorus concentrations between 50 and 300 mg^{-1} kg^{-1} were suitable for growth across sites (Figure 2.32). These soil phosphorus concentrations were similar to those typical of radiata pine plantation forests in New Zealand (Watt *et al.*, 2008; Davis *et al.*, 2015). However, as there are limited studies on the concentrations of soil phosphorus under indigenous forests it is not known whether these sites were deficient in soil phosphorus or other nutrients. An earlier study by Hawkins (1988) investigated how different nutrient treatments affected growth of conifer seedlings in controlled pot experiments. The study corroborated that soil phosphorus was important for growth and mycorrhizae infection can aid growth. However, little research has been conducted in field studies. As the majority of naturally regenerated tōtara sites have established as

young seedlings, it suggests that the sites are likely to have sufficient concentrations of soil phosphorus available for growth, or the trees are likely to have a type of mycorrhizae that may enable them to uptake phosphorus if the available phosphorus concentrations are not sufficient (Baylis, 1969; Hawkins, 1988). The symbiotic association between mycorrhizae and tree species enables the fungi to colonise roots and help with plant uptake of macro and micronutrients (Siddiqui & Pichtel, 2008; Williams *et al.*, 2013). It is not known whether the type of mycorrhizae present on the roots of naturally regenerated tōtara trees enable the species to establish and survive in phosphorus poor soils. Therefore, it would be interesting to investigate what type of mycorrhizae are present on these trees and whether they differ from the planted tōtara sites.

Bray phosphorus and Mehlich 3 extracted phosphorus were not found to be significant in the multiple regression (Table 2.6). However, as the two variables are indicators of soil phosphorus, the multiple regression analysis may have removed the variables due to collinearity. Other nutrients found to be significant to productivity were magnesium, potassium, calcium and manganese (Table 2.5). In previous radiata pine plantation studies, these soil nutrients have been identified as key nutrients that prevent deficiencies (Turner & Lambert, 1986; Watt *et al.*, 2008; Davis *et al.*, 2015). Therefore, these macro and micronutrients are likely to be similar for tōtara and other podocarps in New Zealand (Watt *et al.*, 2008; Davis *et al.*, 2015). Further research should focus on widening the range of soil types included in this study and investigate the soil physical and chemical properties to develop a site fertility classification for planted and naturally regenerated tōtara. This fertility index could be used to identify potential planting sites, and to identify the concentration range of key nutrients (e.g. phosphorus) which are required for growth. This information could be used to identify sites of poor productivity and whether fertiliser application could be used to increase productivity.

For tōtara, the relationship between height (m) and stem diameter (cm) provided an appropriate amount of accuracy to estimate the height of trees based on stem diameter up to a stem diameter of approximately 30 cm (Figure 2.16). This relationship illustrated the variability in tree size and diameter relationships across the 15 study sites. This is potentially influenced by the age of the trees and variable stand densities across sites (Fortin *et al.*, 2019). In forestry, it is common practice

to use these species-specific height-diameter relationships to estimate tree heights as most tree species have strong height-diameter relationships (Vanclay, 2009; Watt & Kirschbaum, 2011; Fortin *et al.*, 2019). Overall, the height model created from these estimated heights using plot specific regression equations provided a strong relationship between height and stem diameter meaning the model is appropriate to use in future studies (Figure 2.17).

The relationship between stand volume (m^3 ha^{-1}) and basal area (m^2 ha^{-1}) was highly correlated (R^2 = 0.90) (Figure 2.26). Stand volume per hectare increased linearly with mean stand basal area (Figure 2.26). Although stand basal area for the sites almost reached 160 m^2 ha^{-1}, it does not appear to have reached the maximum carrying capacity of the stand, which would be identified by a plateau in stand volume. This indicates that the trees are still productive and are not likely to be limited by growing space (Oliver *et al.*, 1994). However, as there are only a few sites with basal areas > 80 m^2 ha^{-1}, more data is needed from sites with basal areas > 100 m^2 ha^{-1} to support this relationship. Additionally, canopy leaf area index (LAI) (m^2 m^{-2}) and basal area (m^2 ha^{-1}) were found to have a positive, linear relationship (Figure 2.29). LAI is often used in forestry and forest ecology to estimate the production of wood in terms of stem volume because LAI is correlated with the stand productivity (Binkley *et al.*, 2013; Mensah *et al.*, 2020). This relationship suggests that sites with a higher LAI (i.e. greater foliage area) are likely to have higher light absorption, which correlates with higher net primary productivity, thus stem growth (Oliver *et al.*, 1994; Penner & Deblonde, 1996; Binkley *et al.*, 2013). The linear increase in LAI and mean stand basal area found in this study suggests that the maximum carrying capacity of tōtara stands has not been reached (Figure 2.29). However, there were only a few sites with mean stand basal areas > 100 m^2 ha^{-1}, therefore more data is required to identify whether tōtara stands above this basal area can have an LAI > 8.

The negative relationship of stand density (stems ha^{-1}) with quadratic mean diameter (cm) across all sites shows that stand density had a strong influence on growth (Figure 2.24 & Figure 2.25). The self-thinning model based on Reineke's SDI approach provided a good indication of the maximum and optimal stand densities for tōtara (Reineke, 1933; VanderSchaaf, 2013). The maximum self-thinning line at 100% relative density provided a good fit to the tōtara dataset as

there were no plots with size-density relationships greater than the 100% line (Figure 2.25). One plot from Site 6 was close to this maximum stand density line which suggests the trees within this stand are likely to have slower growth due to higher intra-specific competition. In theory, mortality is more likely to occur due to higher intra-specific competition between the 55% and 100% relative density lines (Drew & Flewelling, 1977, 1979; Long, 1985). Thinning operations are likely to be needed between these relative densities to maintain the larger tree sizes, or depending on the age of the trees, the stand could be harvested for timber (Drew & Flewelling, 1979; Long, 1985).

The SDI model also indicated that plots below the 35% relative density line were potentially understocked. This suggests that plots below this line have little intra-specific competition and the stands are less likely to require density management for a number of years (Drew & Flewelling, 1977, 1979; Long, 1985). For example, the plot from Site 15 had a stand density of 757 stems ha^{-1} and a D_q of 6.5 cm. At this stand density, the trees are not likely to require density-management until tree growth reaches the 55% line which is approximately at a D_q of 35 cm (Figure 2.24 & Figure 2.25). The SDI model indicated that the majority of plots were at stand densities between the 35% line and 75% relative stand density. The theoretical optimal stocking of the SDI model for tōtara is suggested to be between the 35% understocked stands and 75% fully stocked stands, therefore, the plots around the 55% relative stand density line are likely to have optimal stocking for silviculture (Figure 2.25). To my knowledge this is the first time a SDI model has been developed for tōtara, therefore, this information could be used by landowners and forest managers as a guide for planting and managing tōtara. Compared to an earlier study by Bergin (2001), that identified a coarse site index for tōtara based on volume and age, this SDI model could provide a more informed approach to density management of tōtara stands. Similar to other models, this SDI index will need to be validated to identify whether these self-thinning lines are reliable to use for the management of tōtara. Additionally, it would be beneficial to develop an age/self-thinning model for tōtara which could identify the typical stand densities of tōtara over time. This information could provide more accurate estimates of mortality for growth modelling and could be used to inform landowners and forest managers on the ages and stand densities where natural thinning events occur or where more intense management is required to improve productivity within the tōtara stands.

Another valuable result from this study was the identification of a suitable volume equation to estimate growth variables for tōtara. Previous studies have been unable to quantify the volume and biomass of tōtara without using a proxy for another tree species, or by harvesting individual trees. The equations from Beets *et al.* (2012), Coomes *et al.* (2002), Ellis (1979) and Richardson *et al.* (2009) compared in this study were able to provide reasonable estimates of tree volume and stem biomass for tōtara across sites. However, the equations appeared to over- or under-estimate tree volume and stem biomass compared to the equation from Todoroki and Steward (2019). The volume equation developed by Todoroki and Steward (2019) provided the most appropriate fit to this dataset. This equation was selected because it was specific to the species and developed from a tōtara dataset which had over 451 trees (Todoroki & Steward, 2019). This is an important factor as the majority of equations have not been developed from a dataset of that size. These general volume equations developed by Todoroki & Steward (2019) can be improved by using age specific equations or by adjusting the stump height which occasionally occurs when harvesting naturally regenerated tōtara due to the surrounding areas (Todoroki & Steward, 2019). This result is particularly significant for landowners and future studies as it can improve the accuracy of volume and carbon estimates.

To calculate the above ground biomass of carbon per tree the allometric equation from Beets *et al.* (2012) was used along with the volume equation from Todoroki and Steward (2019) (Equation 2-14). As there were no other values for branch mass and foliage mass available for the species, the allometric equations for mixed species from Beets *et al.* (2012) were used. The branch and foliage biomass of tōtara may be less than the general equations which could lead them to over-estimate carbon. Further research is required before a tōtara specific carbon equation can be developed to ensure that the branch and foliage biomass for the species is being estimated reliably.

Overall, the growth of tōtara in plots at Site 6 and Site 10 indicated that they were the best performing sites in terms of mean stand volume, stem biomass and carbon biomass (Figure 2.19, Figure 2.22 & Figure 2.23). This is potentially due to the age of the trees and low stand densities at these sites. The performance of Site 1 at age 84, Site 4 at age 89, Site 9 at age 60 and Site 11 at age 60 were relatively poor

compared to other sites around the same age (Figure 2.19, Figure 2.22 & Figure 2.23). Low site fertility, competition between species or another site factor(s) could be related to its low productivity. As the productivity at each site excluded competition from other tree species and regenerated tōtara ≤ 10 cm in diameter, some stands may have high levels of inter-specific competition for resources, such as Site 9 where the tōtara trees are at a low stand density, but other trees and vegetation were present and were not measured as they were not in the scope of this study. Site 15 was the worst preforming site, however, this is maybe a result of the young age of the trees. As Site 15 is the youngest site included in this study it is unknown whether the trees were performing poorly due to site factors or due to the age of the trees. It would be interesting to expand this study to incorporate additional sites which are younger than 30 years to identify how the productivity of the sites compare against Site 15. In future studies, if the dataset is large enough, it would be beneficial to investigate the planted and naturally regenerated stands separately to be able to make clear comparisons between variables influencing growth. Planted stands are managed at lower densities with higher initial growth, whereas naturally regenerated stands often develop under nurse species before going through intense competition and disturbance over time (Bergin, 2001). By understanding the different factors influencing growth across the two types of stands, it can help inform the types of management needed to improve the growth of tōtara.

2.5.1 Limitations

One of the main limitations to this study was the lack of accurate age and initial stand density records for the naturally regenerated sites. Further, age was generally only known for one plot for most sites, and the plots at each site were all assumed to be of same age. Naturally regenerated plots are more than likely to include tree cohorts with different ages within the same site as they can establish randomly over time (Bergin, 2000, 2001; Bergin & Kimberley, 2012). However, for some naturally regenerated sites where there was no tree age information available, the age was estimated from anecdotal evidence and growth data. Therefore, to reliably compare the productivity of tōtara across sites it is recommended that the age of each stand should be estimated accurately (Bergin & Kimberley, 2012). It is recommended that each tōtara plot should be aged by obtaining wood increment cores or by growth ring counts from basal discs if trees are harvested (Bergin & Kimberley, 2012).

Another way to improve future studies of tōtara is to increase the frequency of remeasurement (e.g. five-year periods). This information will help provide further accuracy to assessing stand performance, modelling growth and yield and to inform management decisions. This would minimise the number of assumptions which need to be made about each site regarding site history, management and performance. Landowners or forest managers could be trained to carry out the collection of forest mensuration data. However, these recommendations are largely dependent on the cost and man hours the owner and managers are willing to spend on the sites.

Climate data could be collected remotely using temperature, rainfall and soil moisture sensors to identify small scale climate variations which may influence the productivity of tōtara at each site. The VCSN database provided reliable estimates of the climatic data for this study. However, as the data is spatially interpolated across New Zealand daily on a 5 km grid, the large spatial scale of the data may not capture local site variations (e.g. solar radiation, rainfall, soil moisture and humidity) which may influence the productivity of these sites (Chen *et al.*, 1999; Cichota *et al.*, 2008). Further research should be conducted using good quality temperature and soil moisture loggers at each site (Chen *et al.*, 1999).

The multiple linear regression analysis using the backward elimination method selected 11 variables which were significantly related to the productivity of tōtara (Table 2.5). The R^2 of the final model was 0.95 which indicated that the 11 variables retained in the model accounted for 95% of the variability in productivity across sites. This model had the lowest C(p) value of 5.09 and all variables retained in the model were significant to levels equal to or below the selected criteria level of 0.1. Overall, this model provided a good indication of the important climatic and edaphic variables influencing the productivity of tōtara across the study sites. However, as the backward elimination method does not identify the individual R^2 values for the variables retained in the model, it is not known what variables contributed the most to productivity (e.g. mean temperature, rainfall or total phosphorus). It is also likely that collinearity may have been a factor influencing the selection of climatic and soil physiochemical variables in the model (Der & Everitt, 2008). For future research, it is recommended that the multiple regression analysis is tested using the backward elimination method on an independent tōtara

dataset to see if the model identifies similar significant variables or whether the model improves further with a lower C(p) value. To improve our understanding of the backward elimination method additional research is required and it would be useful to conduct a separate analysis prior to the multiple regression to avoid high collinearity between variables. Furthermore, it would also be beneficial to identify the amount each selected variable contributes to the overall regression (e.g. partial R^2 value) to identify the main productivity drivers for tōtara.

Finally, further research on tōtara should focus on increasing the number of representative study sites to incorporate more regions of the North and South Island. With the recommendations mentioned above, this could enable a full analysis to decode why specific sites result in higher productivity than others (e.g. soil texture, soil water, elevation, nutrients, competition or soil moisture).

2.6 Conclusions

In summary, multiple site factors were found to be significant predictors of site productivity of tōtara. Temperature, elevation, rainfall and soil physiochemical properties were the main climatic and edaphic drivers highlighted in this study, however, further investigation is recommended to identify the extent of these relationships on site productivity. It is recommended that any stands of tōtara for which site productivity will be analysed be regularly studied to ensure there is enough information available for a complete analysis (e.g. growth measurements, site history and soil physiochemical properties). This information can be utilised by landowners and forest managers who intend to plant tōtara trees or to manage naturally regenerated tōtara stands for commercial or non-commercial benefits.

2.7 Appendix A

Table 2.7. Soil Textural Information retrieved from Landcare Research's New Zealand Fundamental Soil Layer (FSL) textural classification map.

Site	Soil Texture
1	Clay
2	Clay
3	Clay
4	Clay
5	Clay
6	Clay Loam
7	Clay
8	Clay
9	Sandy Loam
10	Clay Loam
11	Sandy Loam
12	Clay Loam
13	Loamy Sand
14	Loam
15	Clay Loam

Table 2.8. Results of the soil chemistry analysis from soil samples collected from fourteen tōtara sites in 2019. Total C: total carbon; Total N: total nitrogen; Total P: total phosphorus; Bray P: bray phosphorus; Mehlich 3 extracted nutrients; B: boron; Al: aluminium; Na: sodium; Mg: magnesium; P: phosphorus; K: potassium; Ca: calcium; Fe: iron; Mn: manganese; Cu: copper; Zn: zinc.

Site	Total C (%)	Total N (%)	Total P (mg kg^{-1})	Bray P Sequential (mg kg^{-1})			Mehlich 3 Extraction (mg kg^{-1})										
				1	2	3	B	Al	Na	Mg	P	K	Ca	Fe	Mn	Cu	Zn
1/1	3.4	0.3	120.0	4.8	2.8	2.6	0.2	2312.0	11.9	33.8	59.4	61.5	201.0	5.8	86.0	1.7	2.4
1/2	4.5	0.3	92.6	5.0	2.9	2.4	0.2	1580.0	36.8	421.5	9.2	171.0	689.0	17.6	559.0	1.8	1.9
1/3	5.6	0.3	94.5	3.8	2.3	2.0	0.2	1820.0	37.5	460.0	8.7	182.0	763.0	23.3	615.0	2.3	1.9
2/1	4.5	0.3	84.8	4.9	3.1	2.8	0.2	1817.0	45.6	327.3	6.5	186.0	403.0	4.0	528.0	0.8	1.7
2/2	6.4	0.4	106.0	11.9	6.6	5.6	0.2	1911.0	57.0	458.1	5.5	260.0	490.0	4.4	471.0	0.8	1.4
2/3	5.6	0.4	108.0	9.0	4.7	3.8	0.2	1670.0	41.2	221.6	6.9	109.0	514.0	12.7	794.0	1.2	1.5
3/1	6.0	0.4	134.0	8.7	3.9	3.1	0.2	891.0	23.4	173.6	16.4	99.8	371.0	10.1	670.0	0.7	1.9
3/2	5.5	0.3	95.2	6.4	3.4	2.8	0.2	1322.0	31.8	265.5	15.8	189.0	801.0	10.8	575.0	1.6	2.6
3/3	5.9	0.4	156.0	5.6	3.3	2.6	0.2	966.0	44.5	406.9	25.4	292.0	1223.0	102.0	486.0	2.1	4.6
4/1	11.6	0.6	162.0	7.4	4.6	3.7	0.2	1346.0	54.1	500.2	21.6	297.0	1100.0	49.6	728.0	1.9	3.0
4/2	11.5	0.6	185.0	4.6	3.1	2.7	0.2	1353.0	50.3	474.3	13.9	292.0	882.0	61.3	657.0	1.8	3.8
5/1	6.4	0.4	91.8	8.7	4.6	3.6	0.2	2143.0	56.8	354.4	20.2	193.0	643.0	17.3	703.0	0.8	1.6
5/2	6.2	0.4	63.7	7.9	4.2	3.3	0.2	1559.0	28.2	154.7	13.8	120.0	166.0	12.6	470.0	0.9	1.5
5/3	8.9	0.5	113.0	11.4	4.9	3.7	0.2	1379.0	39.9	211.5	12.9	148.0	241.0	29.2	358.0	0.8	2.0
6/1	6.6	0.5	183.0	3.9	2.1	1.7	0.2	943.0	19.9	423.0	8.1	383.0	906.0	322.2	115.0	2.1	2.8
6/2	9.7	0.6	179.0	72.6	43.9	35.5	0.2	1047.0	17.3	268.0	72.8	183.0	1400.0	15.9	683.0	1.1	2.8
6/3	6.6	0.5	296.0	57.0	37.0	30.7	0.2	1286.0	24.9	354.0	103.1	359.0	1473.0	220.8	846.0	2.8	5.1
7/1	7.3	0.5	113.0	23.5	12.8	10.3	0.2	1480.0	60.6	555.4	42.5	407.0	2261.0	20.0	687.0	1.5	4.1
7/2	5.9	0.4	177.0	4.3	2.6	2.1	0.2	944.0	10.7	461.0	10.5	212.0	1068.0	2.6	318.0	1.0	2.8
7/3	6.0	0.4	136.0	4.3	2.0	1.9	0.2	971.0	61.9	582.8	15.3	253.0	1646.0	57.4	545.0	1.3	2.2
8/1	6.2	0.4	145.0	26.7	18.1	15.9	0.2	1289.0	68.5	541.2	11.7	311.0	1491.0	22.2	616.0	1.7	3.2
8/2	6.5	0.4	144.0	41.3	31.3	27.3	0.2	817.0	46.3	319.5	78.7	178.0	1907.0	58.9	782.0	1.4	3.6
8/3	5.7	0.4	105.0	14.6	11.7	8.1	0.2	769.0	61.7	329.2	104.6	156.0	2123.0	28.7	849.0	1.0	3.5
8/4	5.6	0.4	98.8	32.2	22.7	19.7	0.2	463.0	25.5	229.0	34.2	120.0	1334.0	38.2	512.0	1.2	2.9
9/1	5.3	0.3	122.0	4.6	2.8	2.4	0.2	564.0	32.0	228.6	83.7	117.0	1381.0	28.1	837.0	1.2	1.6

Site	Total C (%)	Total N (%)	Total P (mg kg^{-1})	Bray P Sequential (mg kg^{-1})			Mehlich 3 Extraction (mg kg^{-1})									
				1	2	3	B	Al	Na	Mg	P	K	Ca	Fe	Mn	Cu	Zn
9/2	5.6	0.4	136.0	3.4	2.2	2.1	0.2	2852.0	21.6	23.8	3.1	92.4	76.0	5.4	92.0	2.7	1.8
9/3	6.9	0.4	202.0	3.8	2.3	2.1	0.2	2624.0	26.3	33.1	3.3	64.8	194.0	14.3	156.0	1.8	1.7
9/4	5.4	0.4	91.5	3.6	2.1	2.0	0.2	2419.0	27.7	49.0	6.0	99.1	134.0	34.4	459.0	2.8	1.8
10/1	4.4	0.4	141.0	60.3	42.0	38.7	0.2	1949.0	20.9	25.3	5.6	53.2	143.0	18.9	149.0	2.6	2.8
10/2	3.0	0.3	112.0	6.2	4.3	4.0	0.2	1691.0	13.2	188.2	48.8	292.0	973.0	25.3	104.0	0.7	2.6
10/3	4.8	0.4	95.3	22.2	14.6	12.6	0.2	808.0	10.7	383.4	46.5	208.0	1618.0	8.9	395.0	1.3	4.5
11/1	4.0	0.3	135.0	11.6	6.7	5.1	0.2	1615.0	12.0	21.0	10.7	89.3	45.0	13.8	48.0	0.9	2.6
11/2	3.5	0.2	158.0	9.1	4.4	3.3	0.2	1407.0	6.8	16.9	16.2	60.4	46.0	14.0	65.0	0.9	2.7
11/3	3.5	0.2	162.0	8.9	5.6	3.3	0.2	1709.0	9.7	22.1	24.4	88.5	48.0	26.8	99.0	0.8	2.3
12/1	2.8	0.3	213.0	15.1	12.1	11.2	0.2	634.0	18.3	409.2	32.6	213.0	1628.0	16.5	460.0	1.8	3.5
12/2	3.1	0.3	210.0	9.9	5.1	4.1	0.2	918.0	29.1	200.0	21.0	210.0	483.0	50.2	256.0	0.4	2.4
12/3	4.5	0.3	152.0	18.9	10.2	7.5	0.2	970.0	43.9	216.0	40.5	266.0	1045.0	117.3	323.0	0.6	4.3
13/1	9.6	0.5	185.0	16.3	11.8	10.8	0.2	1422.0	16.1	263.1	10.0	202.0	1251.0	40.6	78.0	0.6	3.2
13/2	9.1	0.5	171.0	11.8	7.4	7.0	0.2	1257.0	16.8	241.8	12.2	197.0	1513.0	31.6	75.0	0.5	3.4
13/3	4.6	0.3	135.0	33.6	20.4	17.4	0.2	1392.0	10.3	259.0	33.8	313.0	1242.0	35.2	110.0	0.5	1.5
14/1	6.5	0.5	173.0	28.9	18.6	15.3	0.2	923.0	24.9	322.2	47.6	292.0	1836.0	35.4	391.0	1.5	4.6
14/2	5.3	0.4	226.0	28.8	26.0	12.9	0.2	732.0	31.8	355.4	35.2	247.0	2180.0	34.4	547.0	1.7	4.0
14/3	5.1	0.4	111.0	6.0	6.1	5.5	0.2	1049.0	27.1	362.7	46.9	227.0	1356.0	50.2	513.0	1.2	6.1

Chapter 3

Calibration and Validation of 3-PG for *Podocarpus totara*

3.1 Introduction

The ability of forest tree species to sequester carbon and offset greenhouse gas emissions has made them suitable mitigation strategies to minimise the effects of climate change (Ashton *et al.*, 2012; Mori *et al.*, 2013; Moroni, 2013). These strategies aim to balance carbon sources and sinks to reduce net greenhouse gas emissions (Mori *et al.*, 2013). As a result, legislation in the form of the New Zealand Emissions Trading Scheme (NZ ETS) was created to provide financial incentives to reduce emissions and to comply with global targets (Ministry for the Environment, 2019). In addition to this, government organisations and forestry owners invested in research to identify the key drivers of growth and carbon sequestration in exotic and indigenous tree species to better understand the effects of climate change on the species and how to manage them (Ashton *et al.*, 2012; Covey *et al.*, 2012; Ministry for Primary Industries, 2018). This information is vital to the government's One Billion Tree (OBT) programme which aims to make it easier for landowners to identify suitable locations to plant both exotic and indigenous tree species (Ministry for Primary Industries, 2018, 2019). However, for indigenous tree species there are still substantial knowledge gaps relating to predicting the performance and carbon sequestration of planted and naturally regenerated stands compared to the exotic tree species commonly used in plantation forests (Spittlehouse & Stewart, 2004; Höck *et al.*, 2017; Lin *et al.*, 2018). Forest growth and yield models are tools which have been developed to fill these knowledge gaps to help provide the necessary data to better manage forests and prepare them for future climate scenarios (Pretzsch, 2009). The ability to accurately predict how forests will respond to these scenarios is of great interest to landowners, iwi, forest managers and government.

Forests ecosystems can acclimate to climate change over time, but the extent to which particular species and forest types can change has not been well documented (Spittlehouse & Stewart, 2004; Millar *et al.*, 2007; Williams & Dumroese, 2013).

As the effects of climate change are projected to intensify over the next few decades, forests and forestry systems (i.e. the types of forests we plant and the way we manage them) will need to adapt at a faster rate to survive (Williams & Dumroese, 2013; Ministry for Primary Industries, 2018). Carbon sequestration rates vary between forest types, species and in response to changing climate (Ashton *et al.*, 2012; Covey *et al.*, 2012; Spalding *et al.*, 2012). Exotic and indigenous tree species absorb carbon dioxide from the atmosphere as the species photosynthesise and allocate carbon to biomass (Ashton *et al.*, 2012; Moroni, 2013). The sequestration of carbon can be influenced by biological and physiological factors such as age, stocking, size, nutrient availability and disturbance (Whitehead *et al.*, 2001; Ashton *et al.*, 2012; Spalding *et al.*, 2012). The quantity of carbon in forests is typically related to the stem volume of each tree (Hollinger *et al.*, 1993). The carbon content varies depending on the species, but the majority of studies estimate carbon content as approximately half of the total dry stem biomass (Hollinger *et al.*, 1993; Temesgen *et al.*, 2015). However, the amount of carbon sequestered by each tree over time is largely unknown (Dean *et al.*, 2003; Pretzsch, 2009; Ashton *et al.*, 2012; Temesgen *et al.*, 2015). In New Zealand the majority of commercial plantation species are exotic tree species as they are fast growing, easy to manage for timber production and can produce more than one rotation (crop) over the length of time to grow one rotation of a slower tree species. These species are often considered as solutions to help mitigate carbon dioxide emissions as their carbon uptake over time is rapid (Spalding *et al.*, 2012). However, as they are often harvested with short rotations and have a shorter lifespan compared to indigenous forest species, a large amount of the carbon sequestered during growth is released back into the atmosphere at the time of harvest. Therefore longer-term solutions are needed (Spalding *et al.*, 2012).

A potential long-term solution to mitigate carbon dioxide emissions is the use of suitable indigenous forest species (Höck *et al.*, 2017). As indigenous forest species typically have a longer lifespan than exotic tree species and are not harvested commercially for timber, the species have the potential to be managed for long-term carbon storage solutions. Indigenous forests in New Zealand were estimated to contain 9461 Mt of CO_2 equivalents (Mason *et al.*, 2012; Moroni, 2013). The species in these forests could act as long-term carbon stores, but their growth, productivity and carbon uptake have not been well documented. Currently, the NZ

ETS carbon look-up tables estimate carbon stock per hectare collectively for indigenous forests across all regions of New Zealand (Ministry for Primary Industries, 2017). This is mainly due to the limited information on each indigenous forest species and difficulties quantifying their specific volume and biomass (Kimberley *et al.*, 2014; Steward *et al.*, 2018).

Tōtara is one of these species which could benefit from further research (Höck *et al.*, 2017; Lin *et al.*, 2018). It is estimated that over 150,000 hectares of tōtara exists on private land in the Northland region (Steward *et al.*, 2018). The majority of tōtara stands are used for erosion control, shelter for stock, aesthetics or for wood (Bergin, 2001). Since the introduction of the Forests Management Act in 1949, the harvesting and milling of tōtara has been restricted (Bergin, 2000, 2001). To harvest tōtara on privately owned land a series of permits are required and regulations must be followed before harvesting to ensure the forest stand will not be cleared and an ecological balance will remain (Bergin, 2000, 2001; Allen *et al.*, 2013). This has led to a lag in utilising the species as a commercial timber resource (Steward *et al.*, 2018; Quinlan, 2019). A lack of knowledge around the species, their growth rate and carbon sequestration potential has added to this slow up take (Bergin, 2000, 2001; Steward *et al.*, 2018). However, interest in utilising tōtara has grown over the last 20 years, as landowners and community organisations investigate the potential benefits of selectively harvesting tōtara trees for timber and other resources, or of managing tōtara stands for carbon forestry (Bergin & Kimberley, 2003). Tane's Tree Trust and other organisations created the Northland Tōtara Working Group (NTWG). This group is now collaborating with Te Uru Rākau, Scion and key stake holders on projects such as the Tōtara Industry Pilot (TIP) to research the potential of a sustainable tōtara land-use industry, particularly in the Northland Region (Bergin, 2001; Steward *et al.*, 2018). A key aspect of this research is to fill knowledge gaps about the growth of the species and to identify reliable methods to quantify the timber volume and carbon sequestration potential of stands.

The demand for high value timber, like tōtara, exceeds the current supply because legislative restrictions on harvesting have reduced the supply of timber in New Zealand and regulated the amount of trees for commercial supply (Allen *et al.*, 2013). Overseas imports which were used to fill this market gap were typically from unsustainable forests, therefore incentives to sustainably use naturally regenerated

and/or planted forests on private land have increased. Unfortunately, identifying the commercial value of standing tōtara has been difficult due to the limited information available to quantify wood volume and the unknown costs associated with harvesting and milling the wood (Quinlan, 2011; Quinlan, 2019). In a survey by Quinlan *et al.* (2011) the price of merchantable tōtara was estimated to be similar to macrocarpa pine (*Cupressus macrocarpa* Gordon). The price of timber from tōtara was estimated to be between $135 – $150 per cubic metre at stumpage (Quinlan, 2019). The timber harvested to provide these estimates were from naturally regenerated trees between 80 to 100 years old and the estimates are dependent on the market value of tōtara after milling as the prices vary with the grade of the log (Quinlan, 2011). The harvesting of tōtara trees from privately owned land could potentially bring substantial financial benefits to the regions, along with employment opportunities (Quinlan, 2011). Therefore, the ability to accurately predict the productivity, stand volume and carbon sequestration value of tōtara would be invaluable to landowners, iwi and forest managers. A reliable growth model could be used to quantify the potential of current stands of tōtara for timber and carbon forestry and to provide key information on how to manage future stands.

Forest growth models can be used to provide accurate information to forest managers and government organisations to plan and manage forests for commercial and non-commercial purposes (Vanclay & Skovsgaard, 1997; Amaro *et al.*, 2003). These growth models are not expected to provide perfect predictions, but the higher the accuracy and precision of the predictions, the more reliable the outputs are for forest managers and government to base management decisions off . These models can be assessed by what level of model error is acceptable for operational management of forests (Weiskittel *et al.*, 2011). A key aspect pertaining to the accuracy of this information is the amount of data used to calibrate the model (Vanclay & Skovsgaard, 1997). As empirical growth models are dependent on large quantities of mensuration data from various sites to predict growth, this model type was not suitable for tōtara as there is a limited dataset available for the species (Pinjuv *et al.*, 2006; Pretzsch, 2009; Höck *et al.*, 2017; Lin *et al.*, 2018). Process-based models are more suitable to use with limited datasets as they can account for physiological and environmental variables affecting growth while providing accurate predictions of growth (Pinjuv *et al.*, 2006). These growth models are more

robust and can be used to estimate productivity for sites where trees have not been grown (Landsberg *et al.*, 2003). Therefore, the 3-PG process-based model was selected as it was developed to bridge the gap between empirical and process-based forest growth models (Almeida *et al.*, 2004; Esprey *et al.*, 2004; Sands, 2004). The use of this model could help fill the knowledge gaps surrounding the growth and productivity of tōtara in New Zealand and provide incentives to increase plantings of tōtara and other indigenous forest species within New Zealand.

The 3-PG (physiological processes for predicting growth) model has been used in many countries to model a range of forest species as it is neither species, site or age specific (Landsberg *et al.*, 2003; Sands, 2004). This model can be easily parameterised for new species (Sands & Landsberg, 2002; Esprey *et al.*, 2004; Sands, 2004). The model incorporates five sub models; biomass production, allocation of biomass, stem mortality, soil water, and variables of interest to forest managers such as volume and stand density (Landsberg & Waring, 1997; Sands, 2004). Structurally, the model was developed as an interface which uses Microsoft Excel and an Excel add-in which contains the code for the model to run, therefore it is simple and accessible to use (Sands, 2004). Accurately predicting the productivity of a species is reliant on a series of growth modifiers and site inputs (Nightingale *et al.*, 2008). These growth modifiers include influences for the effect of fertility, frost days and temperature that can all have species specific effects on estimates of biomass productivity and partitioning (Figure 3.1) (Esprey *et al.*, 2004; Sands, 2004; Nightingale *et al.*, 2008). Therefore, these modifiers are crucial to accurately determine outputs (Landsberg *et al.*, 2003; Nightingale *et al.*, 2008).

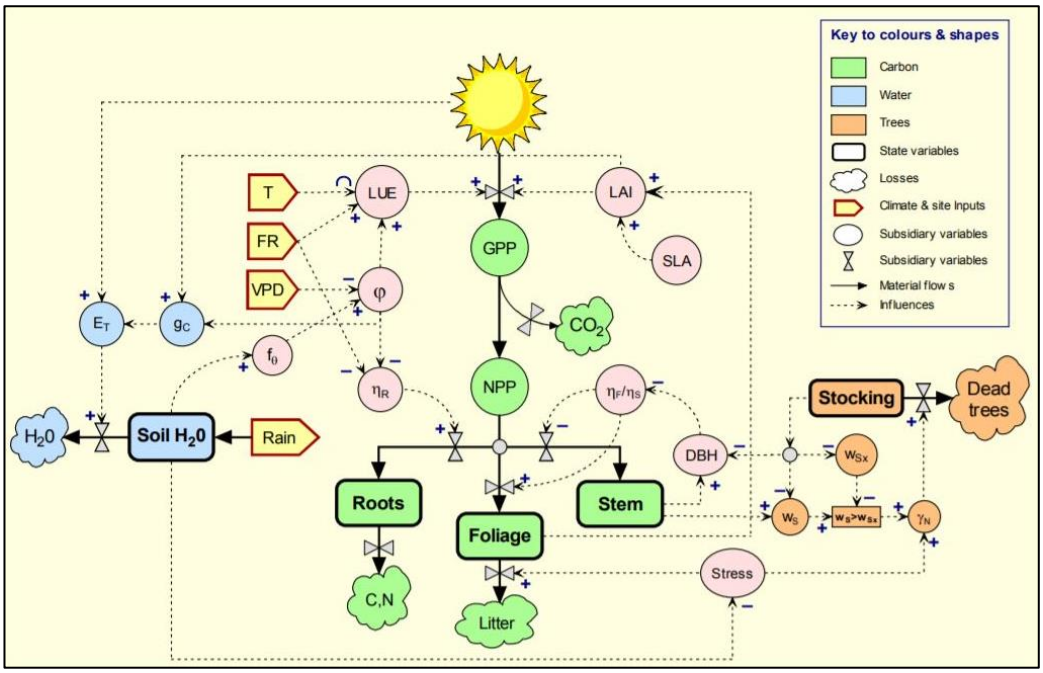


Figure 3.1. The basic structure of the 3-PG forest growth model. Dashed lines indicate the influences between variables which are parameterised for each species (**Table 3.4**) (Sands, 2004).

This model has yet to be applied to tōtara or any other indigenous tree species in New Zealand, meaning there is the potential this model could provide new information which could aid with future management of these species in the face of climate change.

3.2 Objectives

The objectives of this study are to calibrate the 3-PG model to predict the productivity of tōtara by adjusting parameters in the model to fit the calibration dataset. These parameters will be obtained from the literature or estimated from the measured calibration dataset described in Chapter 2. The models results will then be validated against an independent dataset reserved for this purpose to investigate the performance of the model at predicting productivity of tōtara. It is hypothesised that the model will be able to predict the growth of tōtara moderately well, providing a good fit (close to the one to one line) to both the calibration and validation datasets with minimal error (RMSE).

3.3 Methods

3.3.1 Selection of study sites

Data from 21 sites were used to calibrate and validate the model (Figure 3.2). These sites were selected from three forest databases; the Permanent Sample Plot (PSP) database managed by Scion, the Land Use and Carbon Analysis System (LUCAS) database controlled by the Ministry for the Environment (MfE) and the Field Management Approach (FMA) database controlled by the Ministry of Primary Industries (MPI). Fifteen sites were used for calibration and six for validation (Table 3.1 & Figure 3.1). The six validation sites which were not described in Chapter 2 had only historical data available. These data were retrieved from the databases and included some information on age and initial stem density (Table 3.2). Similar to the calibration sites which were described in Chapter 2, the majority of the validation sites were situated on private land, therefore, to keep the data and location of the stands confidential, site descriptions and data are identified by site number (1-21) and region (Table 3.1, Table 3.2 & Figure 3.2).

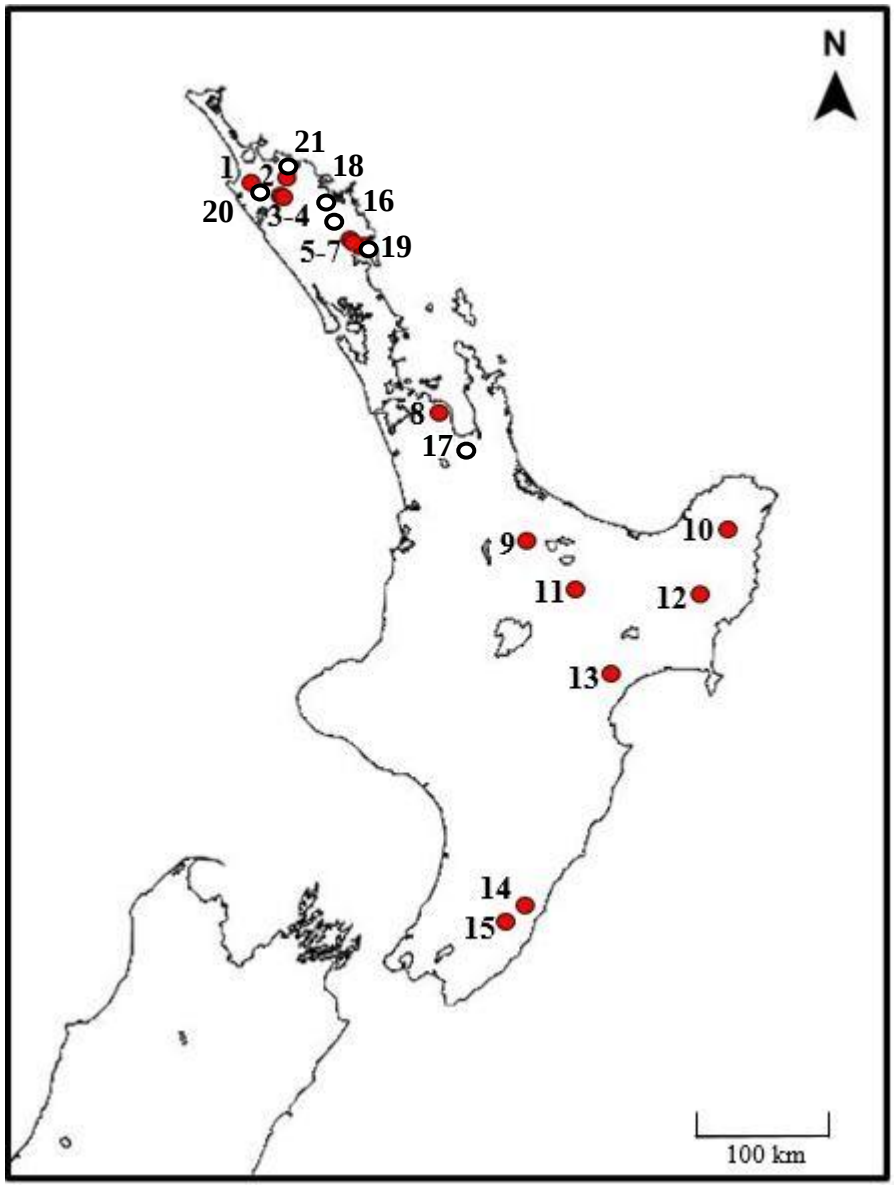


Figure 3.2. Location of the 21 tōtara sites which were used to calibrate and validate the 3-PG model for tōtara.

Table 3.1. Summary of the fifteen sites that were used to calibrate the 3-PG model. Age of the sites is for the year 2019. Min: minimum; Mean ±: standard error; Max: maximum. Mean temperature and Mean total rainfall are annual values.

Site	No. Plots	Size (ha^{-1})	Stocking (stems ha^{-1})	Age (years)	Elevation (m)	DBH (cm)			Height (m)			Mean temp (°C)	Mean total rainfall (mm)
						Min	Mean	Max	Min	Mean	Max		
1	3	0.03	731	84	116	14.17	15.56 ± 1.23	18.01	9.30	10.25 ± 0.61	11.39	14.63	1626.69
2	3	0.03	1462	84	41	16.12	20.03 ± 2.28	24.02	11.94	14.40 ± 2.06	18.50	14.04	1885.11
3	3	0.02	667	89	54	16.38	21.68 ± 2.74	25.50	12.40	14.80 ± 1.61	17.86	14.26	1484.17
4	2	0.03	1387	89	265	14.86	15.08 ± 0.23	15.31	9.76	9.84 ± 0.09	9.93	14.26	1484.17
5	3	0.04	578	69	160	23.09	29.07 ± 3.27	34.37	13.67	13.89 ± 0.19	14.28	14.71	1633.01
6	3	0.03	1236	119	133	21.09	37.38 ± 10.88	58.02	16.95	21.20 ± 2.22	24.46	14.68	1625.47
7	3	0.03	1710	101	64	16.58	18.61 ± 1.73	22.05	10.36	12.90 ± 2.37	17.63	15.07	1473.02
8	8	0.05	2183	30	40	12.68	14.42 ± 0.31	15.48	10.42	10.92 ± 0.09	11.22	13.44	1206.23
9	4	0.04	316	60	561	17.40	20.75 ± 1.60	25.08	11.94	12.87 ± 0.35	13.66	10.57	2287.47
10	3	0.03	417	120	392	27.72	41.63 ± 7.71	54.37	12.33	17.60 ± 2.64	20.5	12.04	1709.79
11	3	0.03	831	60	541	16.33	18.24 ± 1.54	21.30	11.75	12.56 ± 0.40	13.02	10.44	1391.54
12	3	0.03	935	72	150	24.89	26.15 ± 0.91	27.91	15.94	16.65 ± 0.36	17.11	12.89	1069.00
13	3	0.04	1652	86	248	17.69	19.93 ± 1.31	22.21	12.63	14.07 ± 1.00	16.00	12.14	1544.68
14	3	0.03	1197	80	137	17.81	27.75 ± 5.89	38.19	10.88	15.27 ± 2.20	17.56	12.36	1280.25
15	4	0.05	747	10	204	3.17	5.04 ± 1.51	9.55	2.25	2.76 ± 0.39	3.92	12.00	1013.76

Table 3.2. Summary of the six sites that were used for validation of the 3-PG model. Age of the sites is for the year they were last measured (Site 16, 1996; Site 17, 1995; Site 18, 19, 20 & 21, 2008). Min: minimum; Mean ±: standard error; Max: maximum. Mean temperature and Mean total rainfall are annual values.

						DBH (cm)			Height (m)				
Site	No. Plots	Size (ha^{-1})	Stocking (stems ha^{-1})	Age (years)	Elevation (m)	Min	Mean	Max	Min	Mean	Max	Mean temp (°C)	Mean total rainfall (mm)
16	2	0.04	1625	89	260	25.38	29.96 ± 4.58	34.54	19.87	21.42 ± 1.55	22.97	15.22	1489.61
17	1	0.06	1000	70	180	29.05	29.05 ± 1.80	29.05	15.43	15.43 ± 0.58	15.43	12.07	1339.17
18	3	0.04	1445	82	50	14.46	15.73 ± 0.64	16.51	8.80	9.92 ± 0.69	11.11	13.96	1977.04
19	7	0.04	2660	81	80	9.12	12.29 ± 0.88	15.69	7.04	9.37 ± 0.60	11.82	15.04	1335.44
20	4	0.02	1780	73	40	14.45	16.86 ± 1.33	20.65	10.83	11.83 ± 0.52	13.31	14.73	1522.35
21	1	0.03	1273	63	140	11.65	11.65 ± 0.90	11.65	9.61	9.61 ± 0.39	9.61	14.53	1802.97

3.3.1.1 Stand and site descriptions for validation

These six sites included both planted and naturally regenerated tōtara. The ages of these sites ranged from 63 to 89 years old. As these sites were not visited for the present study, the sites were located on Land Information New Zealand (LINZ) Topo50 Map using their GPS coordinates. These coordinates provided soil and climatic information for each site, while the previous site history and descriptions were retrieved from the literature.

3.3.1.1.1 Site 16 – Northland

The two PSPs at this site were planted in 1907 in Puhipuhi, Northland (Figure 3.2 & Figure 3.3) (Bergin, 2001). The stands were planted to provide a long term timber resource option by the Lands Department (Bergin, 2001). The history of this site includes mortality from competition while the stand was younger, fire and cattle damage meaning there was little understory vegetation present (Figure 3.3) (Bergin, 2001). Bergin (2001) established these two PSPs for a previous study.

Figure 3.3. One of the mature stands at Site 16 located in Puhipuhi, Northland (Kimberley *et al.*, 2014).

3.3.1.1.2 Site 17– Waikato

The tōtara at this site are naturally regenerated and found growing on a hillslope in the Kaihere area (Figure 3.2). This PSP is located on privately owned property and is unmanaged with no silvicultural treatments.

3.3.1.1.3 Site 18– Northland

This site was dominated by naturally regenerated tōtara found growing on a moderately steep hill, on privately owned land north of Whakapara (Figure 3.2). The stand density at this site was low as most trees had low branches and multiple leaders (Bergin, 2001). The PSPs had undergone silvicultural treatments of pruning and thinning (Bergin, 2001).

3.3.1.1.4 Site 19– Northland

This tōtara at this site are naturally regenerated and located next to the Whangarei Harbour (Figure 3.2 & Figure 3.4). The coastal site was previously used in a silvicultural trial study where eight PSPs were established on a ridge (Bergin, 2001). The high-density stand was dominated by tōtara trees with some kānuka present (Figure 3.4) (Bergin, 2001).

Figure 3.4. Site 19 before silvicultural treatment was applied. (Photo retrieved from Northland Tōtara Working Group (NTWG)).

3.3.1.1.5 Site 20– Northland

The tōtara at this site are found growing in a tōtara dominant/mixed species stand on a hillslope above the Awaroa River in Herekino (Figure 3.2). Bergin (2001) established four PSPs in the naturally regenerated tōtara stand, located in a grazed paddock on this privately-owned property. Stock were not excluded from grazing this stand, meaning there is little understory vegetation present.

3.3.1.1.6 Site 21– Northland

The tōtara at this site is naturally regenerated and located on private property in the Kaeo area (Figure 3.2 & Figure 3.5). Plots were previously established for the Northland Tōtara Working Group. The stand is located on the hillslope of a large gully. Stock were excluded from the stand. The site has been thinned and pruned as part of management.

Figure 3.5. The tōtara trees at Site 21. (Photo retrieved from Northland Tōtara Working Group (NTWG)).

3.3.2 Climate Data

The 3-PG model required average monthly mean, maximum and minimum temperature (°C), rainfall (mm), solar radiation (megajoules per square metre per day), and frost days (days per month) (Landsberg & Waring, 1997). Climate data for each site were retrieved from the Virtual Climate Stations Network (VCSN). Climate data could only be obtained from 1972 to 2019. As the majority of tōtara

trees were established or planted before 1972, the climate data were repeated through time to provide climate information from 1900 to 2019.

3.3.3 Soil Data

Soil data were retrieved from SMAP and Landcare Research using GPS coordinates. The data were obtained from Landcare Research's New Zealand Fundamental Soil Layer (FSL) textural classification map with a 100 m resolution (Appendix B, Table 3.3) (Meason *et al.*, 2011). Plant available soil water data were obtained from the same FSL (Palmer *et al.*, 2009).

3.3.4 Statistical Analysis

As heights were not available for all stems within each PSP, heights were estimated for all stems by using non-linear power regression equations following the method described in Chapter 2. All trees included in this study were assumed to be mature tōtara trees. Trees with a stem diameter of < 10 cm at breast height were excluded from the analysis to prevent young self-established individuals from skewing the merchantable stem information. Site 15 was not altered due to the young age of the site. The basal area, volume, mean annual increment and stem density were calculated following the method described in Chapter 2. The equation from Todoroki and Steward (2019) was used to calculate stand volume. The stand density of the plots determined whether the plots at each site were separated or kept together for modelling. We assumed plots from the same site with similar stand histories would have similar growth, therefore the plots at each site were combined if their stem densities did not differ by more than 150 stems ha^{-1}. If the plots differed > 150 stems ha^{-1} the growth of each plot was modelled separately.

3.3.5 Model Parameterisation

As the 3-PG model had not been used for tōtara before, parameterisation and calibration of the model was required (Appendix B, Table 3.4). The Microsoft Excel Interface 3-PGpjs Version 2.7 was used to parameterise, calibrate and validate the 3-PG growth model to tōtara. Literature was used to identify key values which were suitable as input parameters for tōtara to parameterise the model. Parameters which were unable to be obtained from direct measurements or from the literature were

set to default values which were obtained from the previous parameterisations for Radiata pine (*Pinus radiata*) (Landsberg *et al.*, 2003; Paul *et al.*, 2003) and Sitka spruce (*Picea sitchensis*) (Minunno *et al.*, 2010). The process of calibration involved running the model and adjusting the parameters to improve the fit of model to the observed data across all calibration sites simultaneously until a better fit was achieved. By running multiple sites at once and not adjusting the parameters on a site by site basis it removed bias from adjusting the parameters until the closest fit was achieved for sites. The parameters which were adjusted to improve the fit to the calibration data included the specific leaf area values, self-thinning functions and the temperature, frost and fertility modifiers.

3.3.5.1 Allometric relationships & partitioning

The foliage to stem partitioning ratios for tōtara at stem diameters of 2 cm and 20 cm (pFS2 and pFS20) were estimated from calculations obtained from the literature (Coomes *et al.*, 2002; Marden *et al.*, 2018). Allometric equations specific to tōtara from Marden *et al.* (2018) were used to calculated the foliage to stem partitioning ratio at a stem diameter of 2 cm (PFS2) (Equation 3-1 & Equation 3-2). This study examined the biomass and root attributes of tōtara and other common indigenous forest species within their first 5 years of establishment (Marden *et al.*, 2018). The outputs from allometric equations were converted to cm. Foliage biomass ($B_{(f2)}$) was calculated for pFS2 as:

$$B_{(f2)} = 51.688 \exp(0.049D) \quad (3\text{-}1)$$

where $B_{(f)}$ is foliage biomass and D is stem diameter at (2 cm). The stem biomass component was calculated using the following equation:

$$B_{(s2)} = 39.461 \exp(0.052D) \quad (3\text{-}2)$$

where $B_{(s)}$ is the stem biomass and D is stem diameter (2 cm). The value for pFS2 was calculated by dividing $B_{(f2)}$ by $B_{(s2)}$ (Equation 3-1, Equation 3-2 & Table 3.4). To estimate the foliage to stem partitioning ratio at a stem diameter of 20 cm (pFS20), modified equations from Coomes *et al.* (2002) were used. To determine the height (m) at a stem diameter of 20 cm, the non-linear relationship between stem diameter (cm) and height (m) from the tōtara calibration dataset were used (Figure

2.18). The height at a stem diameter of 20 cm was 15.5 m. The mean species specific wood density (ρ) for tōtara was estimated from a study by Steward and McKinley (2019). The mean wood density for tōtara was 443 kg m^3 (Steward & McKinley, 2019). The stem biomass component was estimated as:

$$B_{(s20)} = 0.0000598\rho D^2 H \quad (3\text{-}3)$$

where D is stem diameter (20 cm), H is and height (15.5 m) and ρ is the species-specific wood density (443 kg m^3). The foliage biomass component was estimated as:

$$B_{(f20)} = 0.0406 D^{1.53} \quad (3\text{-}4)$$

where D is stem diameter (cm). The pFS20 was calculated by dividing $B_{(f20)}$ by $B_{(s20)}$ (Equation 3-3, Equation 3-4 & Table 3.4). The stem mass versus stem diameter relationship was calculated using the calibration dataset. The constant and power (aS and nS) of this relationship was calculated as:

$$B_{(s)} = 0.0455 D^{2.5243} \quad (3\text{-}5)$$

where D is stem diameter (cm). The maximum and minimum fraction of net primary productivity to roots (pRx and pRn) were obtained from radiata pine as no other values were available for root partitioning for tōtara.

3.3.5.2 NPP and Conductance Modifiers

The temperature modifier in the model required the minimum, optimum and maximum temperatures tōtara can grow at. As there is little information available regarding temperatures for growth of tōtara, the values were estimated from the literature. The optimal growth temperature (27°C) for tōtara was obtained from a study by Hawkins (1988) that analysed the physiology and genetics of rimu, kahikatea and tōtara. The minimum and maximum temperatures were estimated by testing the sensitivity of the model growth outputs to temperature. A minimum of 5°C and maximum of 35°C to account for the warmer northern growing sites were selected based on this approach. The frost modifier (fFRost) in the model assumes

that no photosynthesis will occur for a specified number of days (kF) after the temperature drops below zero degrees (Landsberg & Waring, 1997). The modifier was initially set to 1 kF and was later adjusted during calibration to 3 kF.

3.3.5.3 Stem Mortality & Self-thinning

The initial maximum stem mass per tree at 1000 trees per hectare (wSx1000) was input at 562 kg tree^{-1}. This value was later adjusted to 900 kg tree^{-1} to fit the calibration dataset. The power of the self-thinning law for tōtara trees was estimated using the following equation from the relationship between stand density and stem diameter:

$$SD = 174{D_q}^{-1.42} \quad (3\text{-}6)$$

where SD is stand density (stems ha^{-1}) and D_q is quadratic mean diameter (cm).

3.3.5.4 Canopy structure and processes

The specific leaf area (SLA) value for mature tōtara leaves was obtained from a study by Simpson *et al.* (2016). This study measured traits from 64 indigenous tree species in New Zealand including tōtara (Simpson *et al.*, 2016). The SLA value of 5.46 mm^2 mg^{-1} was measured in the study by sampling mature, well-lit leaves (Simpson *et al.*, 2016). Two more SLA measurements were found for tōtara in the literature from studies by White and Scott (2006) and Jager *et al.* (2015). The SLA value from Simpson *et al.* (2016) was selected as it was the most relevant to this study having measured the SLA of mature tōtara trees and because it provided the median SLA between the values obtained from the literature. The SLA value for trees at age 0 was assumed to be the same as radiata pine at 11 mm^2 mg^{-1}.

3.3.5.5 Wood and stand properties

The stem height allometric relationship was calculated by using a non-linear regression curve fit to the stem height (m) versus diameter (cm) relationship of all trees (Figure 3.8). The following equation provided the parameter values:

$$H = 1.41D^{0.73} \quad (3\text{-}7)$$

where H is height (m) and D is stem diameter (cm). To calculate the stem volume allometric relationship (aV and nVB), a regression of mean stem diameter (cm) versus mean volume of the calibration dataset was used (m^3 ha^{-1}) (Figure 3.9). The following equation from the non-linear regression provided the parameter value for this allometric relationship:

$$V = 0.98D^{1.86} \quad (3\text{-}8)$$

where V is volume m^3 ha^{-1} and D is stem diameter (cm). The conversion factors were not adjusted at any stage.

3.3.6 Model Calibration

Calibration of the 3-PG model to tōtara was achieved by testing to see how the predictions from the model with the chosen parameterised values, fitted the calibration data (Table 3.1). From the first run of the model, 3-PG was able to provide estimates of growth for tōtara but, there were a few adjustments that were needed to improve the fit of the model. The initial parameter value of 5.46 mm^2 mg^{-1} for SLA of mature trees was retrieved from the literature, but due to the model under-estimating the measured leaf area index data from the calibration sites, the SLA value was increased to 18 mm^2 mg^{-1}. The SLA value for trees at age 0 was increased from 11 mm^2 mg^{-1} to 20 mm^2 mg^{-1}. These adjustments enabled the model to predict the canopy leaf area more accurately. As the self-thinning parameter was over-estimating stand density at all sites, the power value was adjusted to 1.2 by fitting the model to the calibration dataset. For the sites where silvicultural history (e.g. actual stand densities) was known, the data was input into the thinning parameter box to help the model predict volume and basal area more accurately. However, for the sites where limited silvicultural history was available (e.g. naturally regenerated sites) the thinning history was estimated based on the general assumptions that intra-specific competition occurred as the individuals increased in stem diameter. The fertility modifier (FR) in the model ranged from 0 to 1, where sites were assumed to be infertile at 0 and highly fertile at 1 (Landsberg *et al.*, 2001; Landsberg *et al.*, 2003; Sands, 2004). The parameter value for the fertility modifier was set at 0.6 as we assumed all sites had a moderate level of fertility. After the

other parameters were adjusted, the individual fertility rating at each site was adjusted between 0.2 and 0.7 to account for the differences between the observed and predicted outputs which the model was unable to explain by the other parameters.

Once the model was calibrated, a multisite analysis was performed to run all sites simultaneously. The multisite analysis enabled the calibration dataset to be compared against a one-to-one line to measure how well the model estimated productivity of stem diameter, basal area, volume, height and stand density. Figure 3.6 shows the predicted outputs from one of the calibration sites after adjustments were performed.

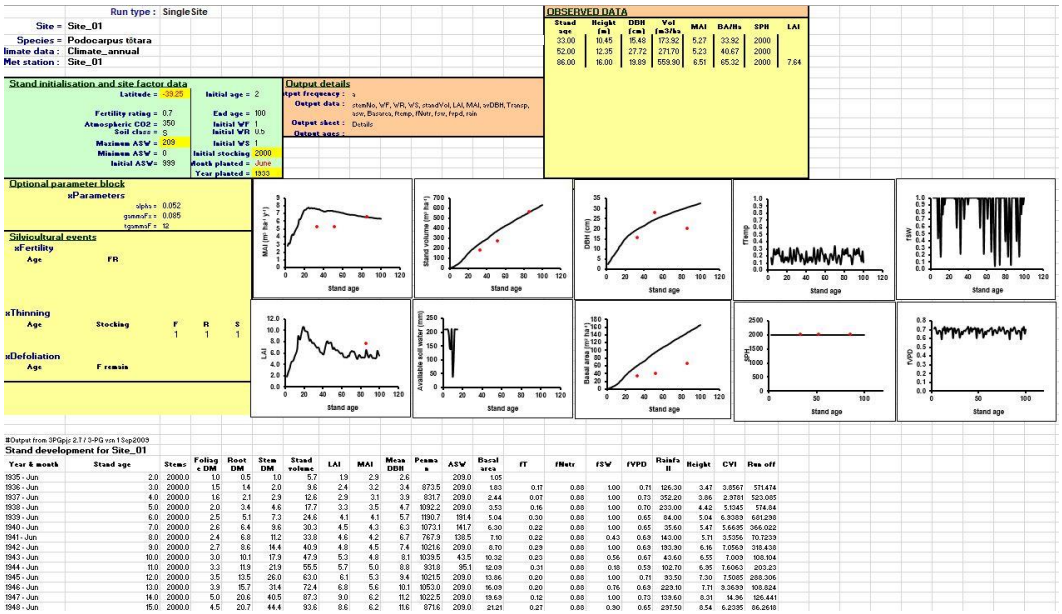


Figure 3.6. Example of the 3-PG model interface used to calibrate the model to each site.

3.3.7 Validation of 3-PG

The performance of the model was tested by simulating the growth of an independent dataset not used for calibration (Table 3.2). Information regarding the silvicultural management of these validation sites was obtained from previous historical data where available. For sites where there was little information about stand density, assumptions were made to fit the current data. For example, the initial stand density of naturally regenerated sites was assumed to be 6000 stems ha^{-1}. This assumption was based on the previous knowledge that naturally regenerated tōtara stands usually have very high stem densities at young ages before natural mortality

or silvicultural management occur (Bergin, 2000). The fertility rating for each validation site was based on the assumption that all sites were reasonably fertile, therefore the fertility ratings were adjusted between 0.2 and 0.7 to account for the differences between the observed and predicted outputs.

3.3.8 Analysis of performance

The residuals were calculated by subtracting the mean observed values from the mean predicted values. To then quantify the percent the model over- or under-estimated the outputs this residual value was then divided by the mean observed value. Additionally, the coefficient of determination (R^2) of regression and root mean square error ($RMSE$) were used to assess the performance of the model when comparing observed verse predicted values. The RMSE was calculated for each predicted variable to quantify the accuracy of the models' predictions (Chai & Draxler, 2014). This was calculated using the following equation:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(y_i - \hat{y}_i)^2}{n-1}} \quad (3\text{-}9)$$

where y_i and $\hat{y}_i$ are observed and predicted values, n is sample size and 1 is the number of independent variables. High R^2 and low values of RMSE indicate better model predictions of the observed response (Chai & Draxler, 2014).

3.4 Results

3.4.1 Calculation of model parameter values

The 3-PG model assumes a power relationship for mortality with stand tree density and mean tree stem diameter. The mortality 3-PG parameter power value (thinPower) was calculated by first plotting the mean stand density (stems ha^{-1}) and mean quadratic mean diameter (cm) of each plot from the calibration dataset (Figure 3.7). Then a power regression equation was fitted to the points that represent the highest possible density observed for a given mean diameter, thinPower = 1.42 (Figure 3.7).

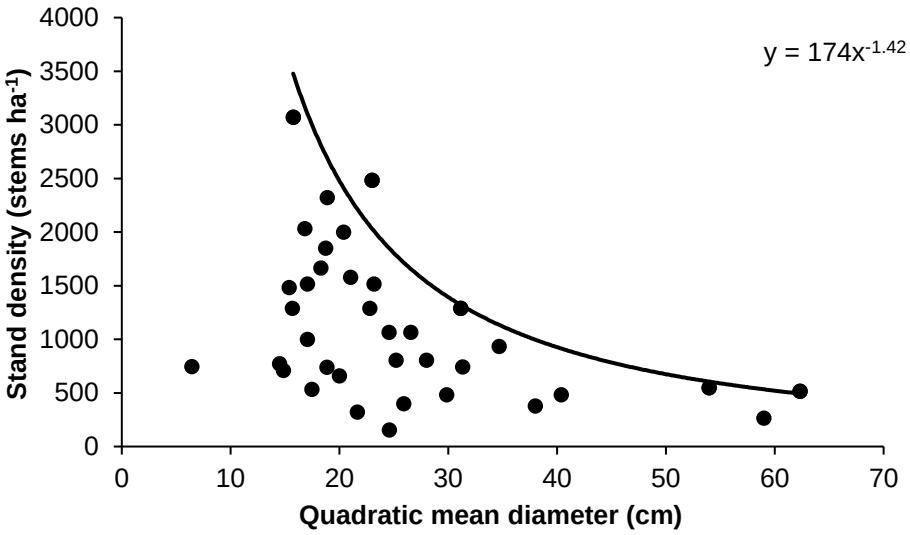


Figure 3.7. Non-linear relationship between stand density (stems ha^{-1}) and quadratic mean diameter (cm) of each plot from the calibration dataset. Solid line represents the regression fitted as a boundary line to represent the highest possible density observed for a given mean diameter (Equation 3-6).

The stem height allometric relationship in the 3-PG model assumes a power relationship for stem height (m) (Figure 3.8). The stem height relationship was calculated by plotting the mean height (m) and mean stem diameter (cm) of each plot in the calibration dataset (Figure 3.8). Then a power regression equation was fitted to provide the parameter values of aH = 1.41 and nHB = 0.73 (R^2 = 0.76) (Figure 3.8).

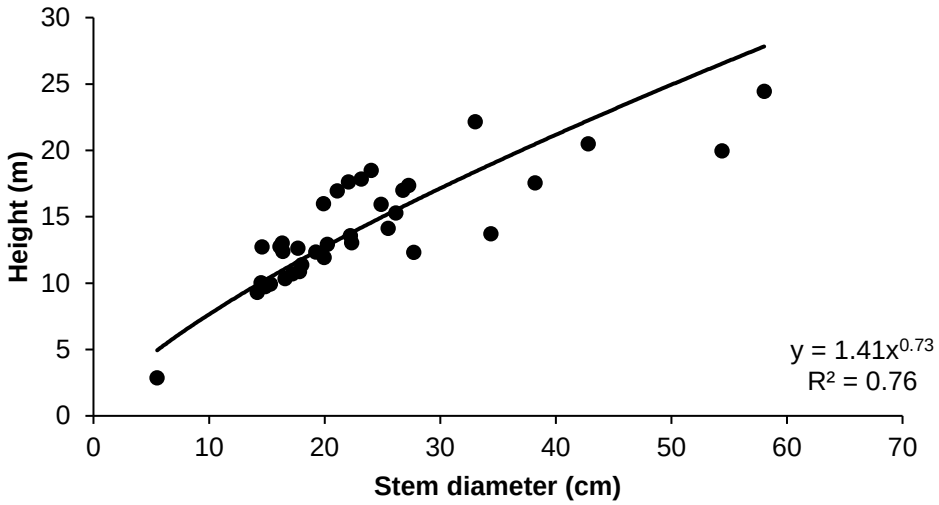


Figure 3.8. Stem height allometric relationship between height (m) and stem diameter (cm) of each plot from the calibration dataset. Solid line represents the regression (R^2 = 0.76).

The 3-PG model assumes a power relationship for the stem volume allometric relationship. The stem volume relationship was calculated by plotting mean volume (m^3 ha^{-1}) and mean stem diameter (cm) of each plot (Figure 3.9). Then a power regression equation was fitted to provide the parameter values of aV = 0.98 and nVB = 1.86 (R^2 = 0.64) (Figure 3.9).

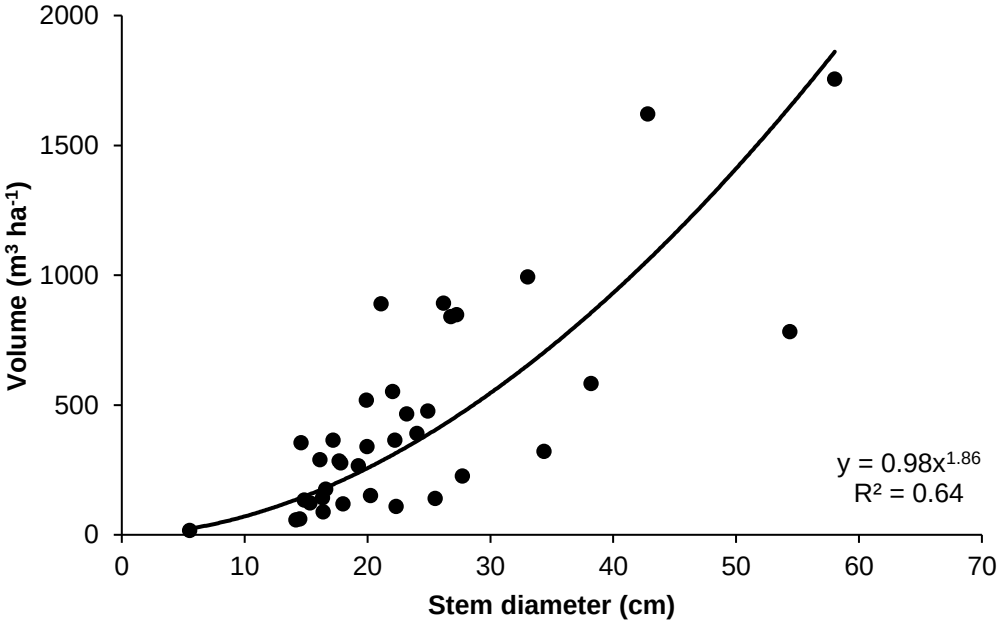


Figure 3.9. Stem volume allometric relationship between mean volume (m^3 ha^{-1}) and mean stem diameter (cm) of each plot from the calibration sites. Solid line represents the regression (R^2 = 0.64).

3.4.2 Calibration of 3-PG

The 3-PG model was able to predict mean stem diameter moderately well with an $R^2 = 0.64$ and RMSE = 9 cm (Figure 3.10). Overall, the model over-estimated mean stem diameter by 32% (Figure 3.10). The model over-estimated mean stem diameter of older sites with stem diameters ≥ 10 cm by 24% (Figure 3.10).

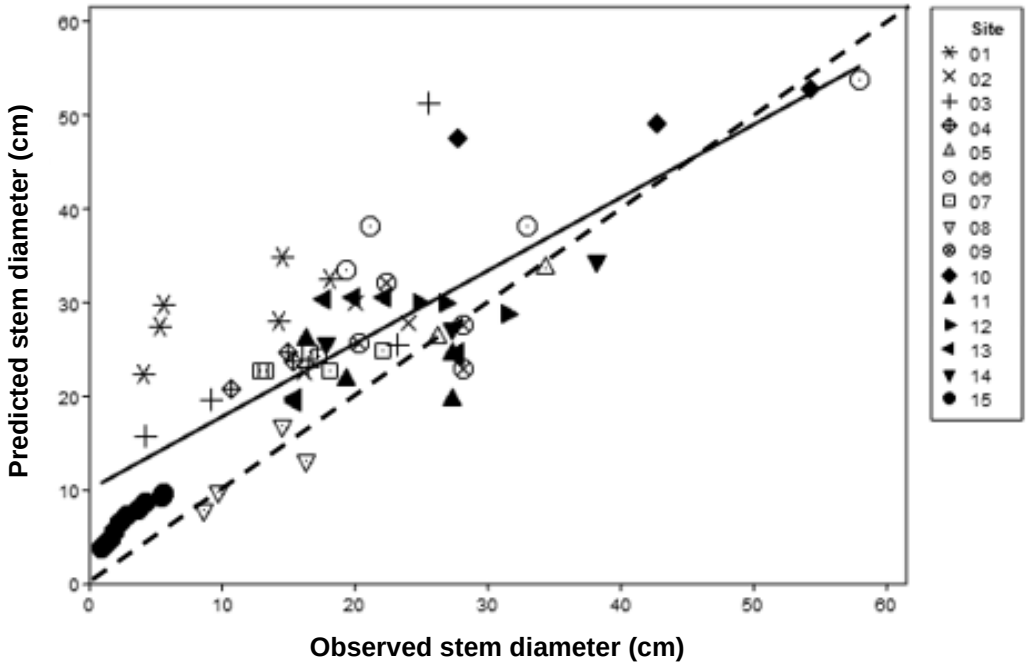


Figure 3.10. Relationship between mean observed and predicted stem diameter (cm) for the fifteen calibration sites. The solid black line represents the regression line (—) (R^2 = 0.64, RMSE = 9 cm). The dashed line represents the one-to-one line (- - -).

The model explained less of the variability for mean basal area with an $R^2 = 0.21$ and RMSE = 137 $m^2\,ha^{-1}$ (Figure 3.11). The majority of sites were scattered either side of the one to one line, as the model predicted only 21% of the variation meaning a large portion of the variation in the data was not explained (Figure 3.11). The model over-estimated mean basal area by 64% across all calibration sites (Figure 3.11). At sites with low basal area (e.g. Site 1 and Site 7) the model over-estimated basal area (Figure 3.11). The RMSE value of 137 $m^2\,ha^{-1}$ was high for the range of observed basal area between 0 to 200 $m^2\,ha^{-1}$, indicating a low accuracy for 3-PG basal area predictions (Figure 3.11).

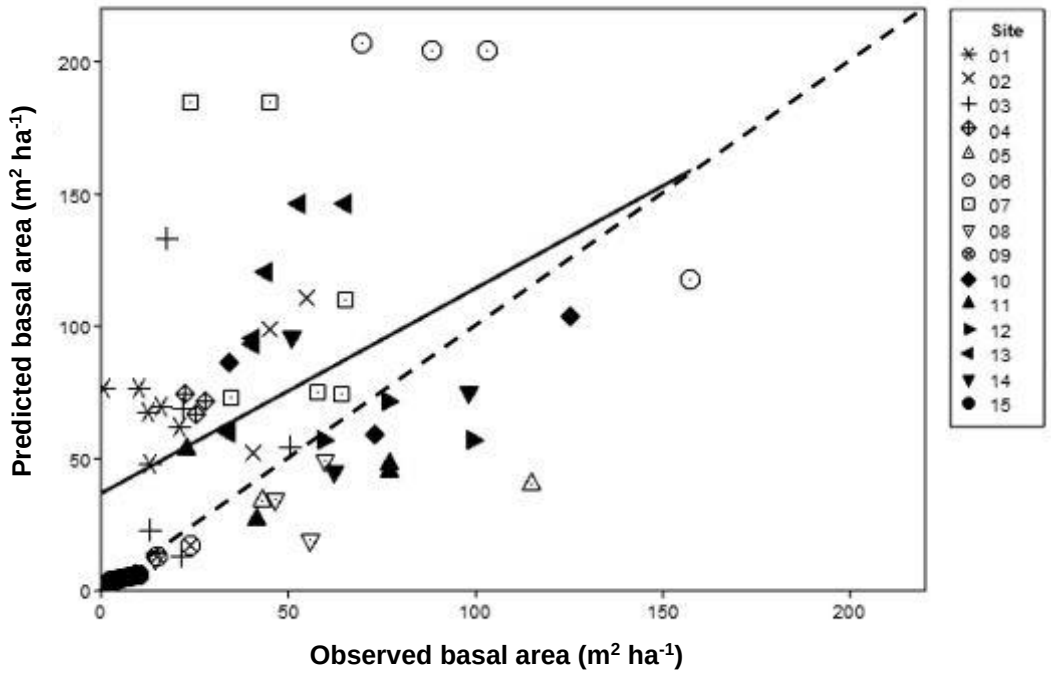


Figure 3.11. Relationship between mean observed and predicted basal area ($m^2\ ha^{-1}$) for the fifteen calibration sites. The solid black line represents the regression line (—) (R^2 = 0.21, RMSE = 137 $m^2\ ha^{-1}$). The dashed line represents the one-to-one line (- - -).

The 3-PG model predicted mean volume better than mean basal area, with an R^2 = 0.43 and RMSE = 312 $m^3\ ha^{-1}$ (Figure 3.12). At Sites 1, 3 and 10, the model tended to over-estimate volume; these were older sites with low volumes (≤ 250 $m^3\ ha^{-1}$) (Figure 3.12). The majority of sites remained close to the one to one line. Overall, the model over-estimated mean volume across all calibration sites by 43%, however, this average was probably skewed by the large over-predictions of the sites with low volumes (Figure 3.12).

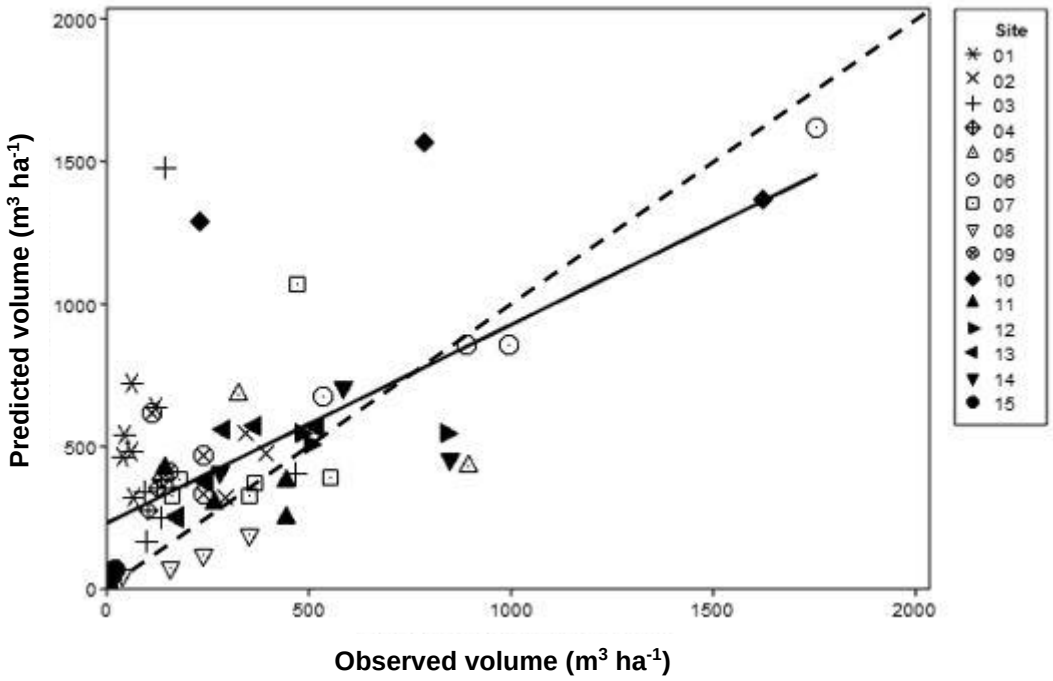


Figure 3.12. Relationship between mean observed and predicted volume ($m^3\,ha^{-1}$) for the fifteen calibration sites. The solid black line represents the regression line (—) ($R^2 = 0.43$, RMSE = 312 $m^3\,ha^{-1}$). The dashed line represents the one-to-one line (- - -).

The relationship between observed and predicted height was moderately strong with an $R^2 = 0.68$ and RMSE = 4.5 m (Figure 3.13). The model over-estimated mean heights as the majority of sites were situated above the one to one line (Figure 3.13). Mean heights at sites with low stand densities seem to be over-estimated by the model (e.g. Site 1, 3 and 10) (Figure 3.13 & Table 3.1). Overall, the model over-estimated mean height across all calibration sites by 29% (Figure 3.13).

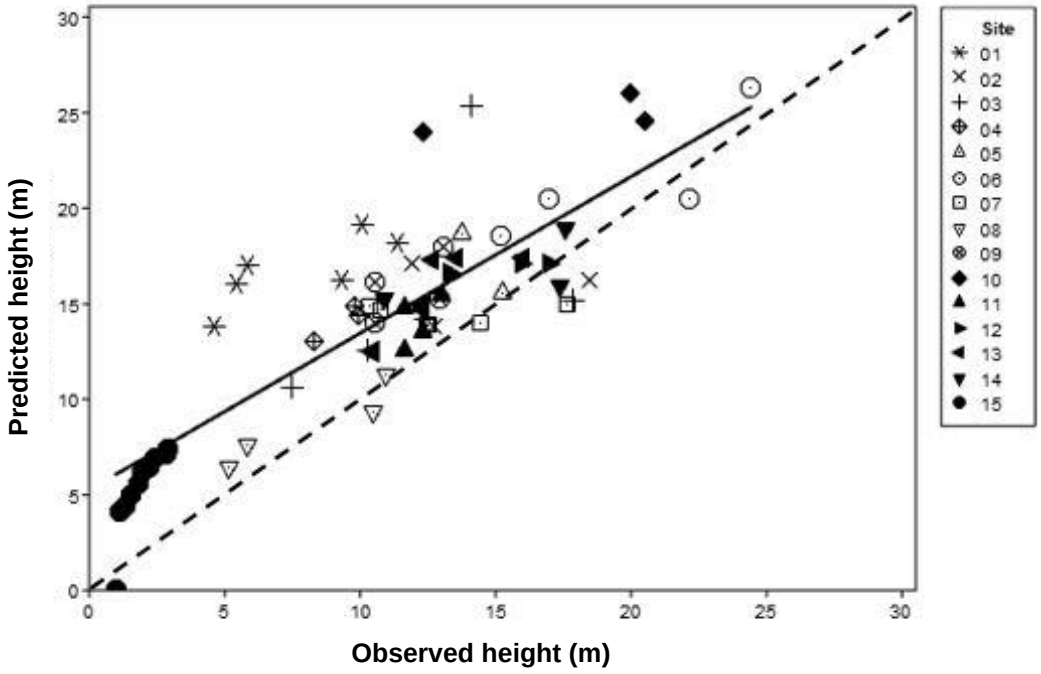


Figure 3.13. Relationship between mean observed and predicted height (m) for the fifteen calibration sites. The solid black line represents the regression line (—) (R^2 = 0.68, RMSE = 4.5 m). The dashed line represents the one-to-one line (- - -).

The strongest relationship from the model was between mean observed and predicted stand density with an R^2 = 0.76 and RMSE = 594 stems ha^{-1} (Figure 3.14). The model provided a good fit to the observed calibration data as the majority of sites were close to the one to one line (Figure 3.14). Overall, the model over-estimated mean stand density across all calibration sites by 11% (Figure 3.14). However, at Site 7, mean stand density was over-estimated by 54%, this could probably be explained by the lack of site history data for this site (Figure 3.14).

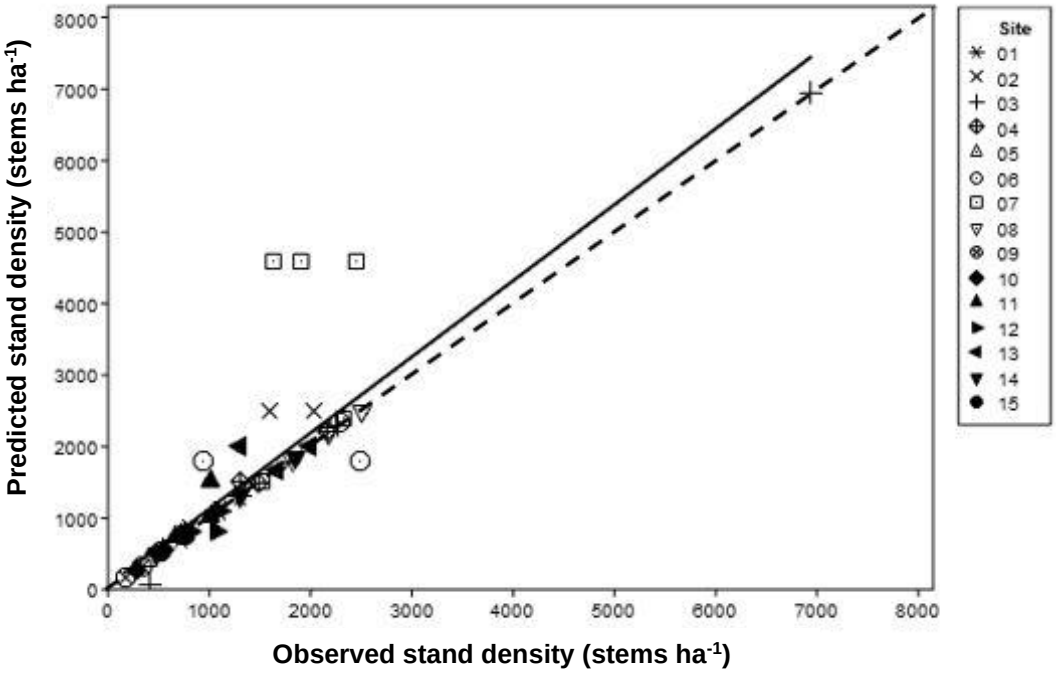


Figure 3.14. Relationship between mean observed and predicted stand density (stems ha^{-1}) for fifteen calibration sites. The solid black line represents the regression line (—) (R^2 = 0.76, RMSE = 594 stems ha^{-1}). The dashed line represents the one-to-one line (- - -).

Overall, the calibrated 3-PG model was able to predict mean stem diameter, basal area, volume, height and stand density across the calibration sites with varying degrees of accuracy. The model performed reasonably well with the calibration data, with moderately strong relationships and low RMSE for mean stem diameter, mean height and mean stand density (Figure 3.10, Figure 3.13 & Figure 3.14). The model's fit to mean basal area and mean volume data from the calibration sites was not as strong (low R^2 and high RMSE) but, it did provide some explanation for the variation in growth across the calibration dataset (Figure 3.11 & Figure 3.12).

3.4.3 Validation of 3-PG

The performance of the model was more variable when tested with the validation dataset. The model over-estimated mean stem diameter, mean basal area, mean volume and mean height for four of the six validation sites (Figure 3.15, Figure 3.16, Figure 3.17 & Figure 3.18). However, the model provided a good fit to mean stand density for all validation sites (Figure 3.19). Two validation sites (Site 16 & Site 17) with large tree diameters, but low stand density, were consistently under-estimated by the model for the majority of growth variables. These sites were removed from the validation dataset to test if the regression results from the model improved for any of the growth variables.

The relationship between observed and predicted mean stem diameter (cm) was weak with an $R^2 = 0.08$ and RMSE = 10.3 cm (Figure 3.15). The model over-estimated stem diameter at validation sites with smaller mean stem diameters (≤ 20 cm) by 74% (Figure 3.15). Sites with large mean stem diameters (≥ 30 cm) were under-estimated by 29% (Figure 3.15). The removal of the two outliers (Site 16 & Site 17) improved the regression relationship for the remaining validation sites, resulting in an $R^2 = 0.25$ (Figure 3.15).

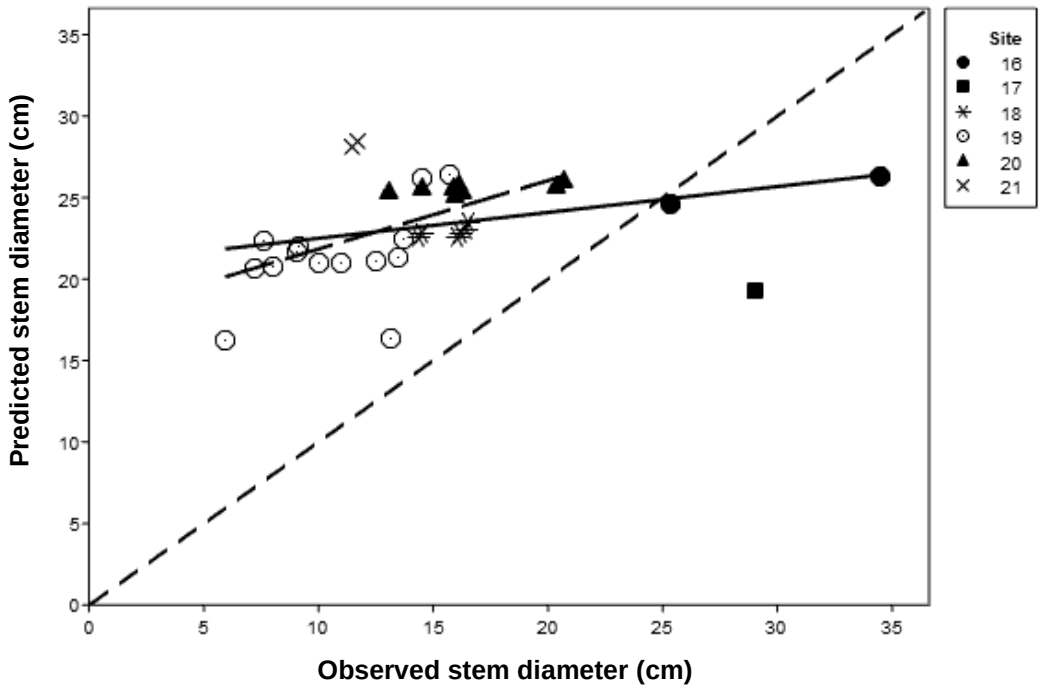


Figure 3.15. Relationship between mean observed and predicted stem diameter (cm) for the six validation sites. The solid black line represents the regression line (—) ($R^2 = 0.08$, RMSE 10.3 cm). The dashed line represents the one-to-one line (- - -). The solid dashed black line represents the regression with Sites 16 and Site 17 removed ($R^2 = 0.25$, RMSE 10.6 cm).

The model was unable to predict observed mean basal area across all validation sites, resulting in an R^2 = 0 and RMSE = 86 $m^2\ ha^{-1}$ (Figure 3.16). Overall, the model over-estimated mean basal area by 183% (Figure 3.16). The regression results from the model improved slightly when outliers were removed (R^2 = 0.07, RMSE=89 $m^2\ ha^{-1}$).

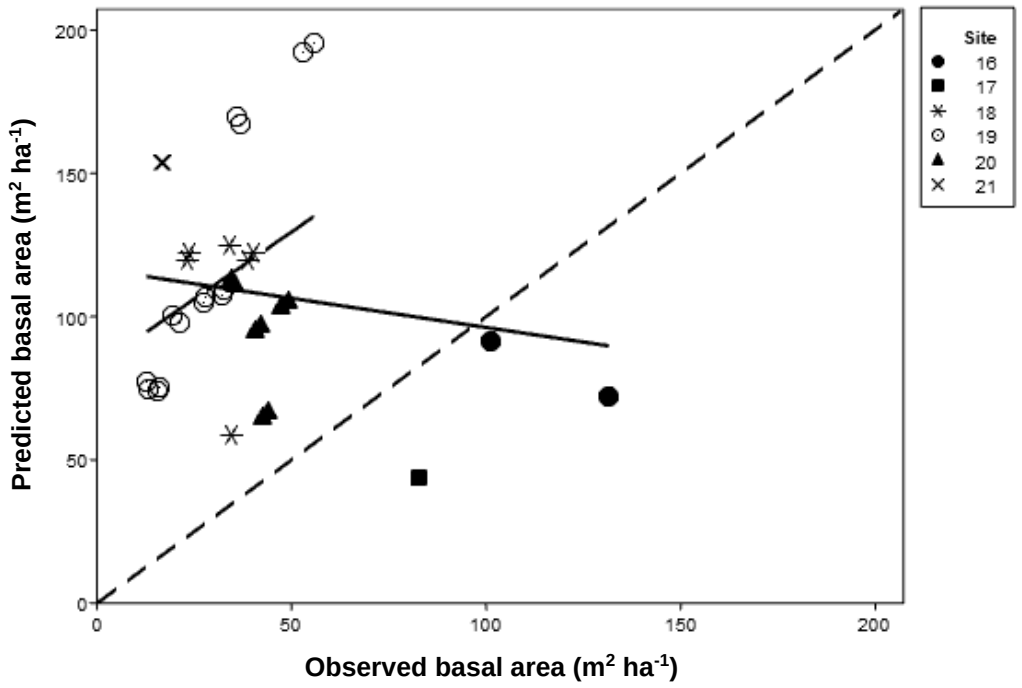


Figure 3.16. Relationship between mean observed and predicted basal area ($m^2\ ha^{-1}$) for the six validation sites. The solid black line represents the regression line (—) (R^2 = 0, RMSE 86 $m^2\ ha^{-1}$). The dashed line represents the one-to one line (- - -). The solid dashed black line represents the regression with Sites 16 and Site 17 removed (R^2 =0.07, RMSE 89 $m^2\ ha^{-1}$).

Similar to mean basal area, the model was unable to accurately predict mean volume across sites from the validation dataset (R^2 = 0, RMSE = 185 $m^3\ ha^{-1}$) (Figure 3.17). Overall the model over-estimated mean volume by 76% (Figure 3.17). The regression results from the model did not improve after the outliers were removed (R^2 = 0.01, RMSE = 314 $m^3\ ha^{-1}$).

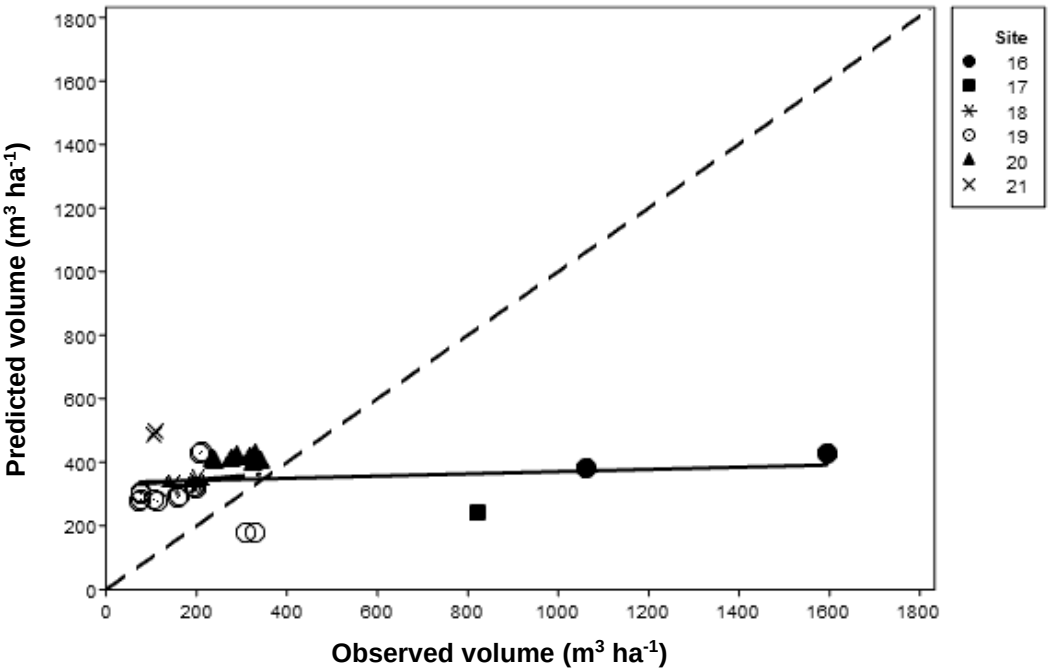


Figure 3.17. Relationship between mean observed and predicted volume ($m^3 ha^{-1}$) for the six validation sites. The solid black line represents the regression line (—) (R^2 = 0, RMSE = 314 $m^3 ha^{-1}$). The dashed line represents the one-to one line (- - -), and the solid dashed black line represents the regression with Sites 16 and Site 17 removed (R^2 =0.01, RMSE = 185 $m^3 ha^{-1}$).

There was a weak relationship between mean observed and predicted height (R^2 = 0.06, RMSE = 4.7 m) (Figure 3.18). Overall, the model over-estimated mean height across the validation sites by 31% (Figure 3.18). The regression results from the model did not improve after the outliers were removed (Figure 3.18).

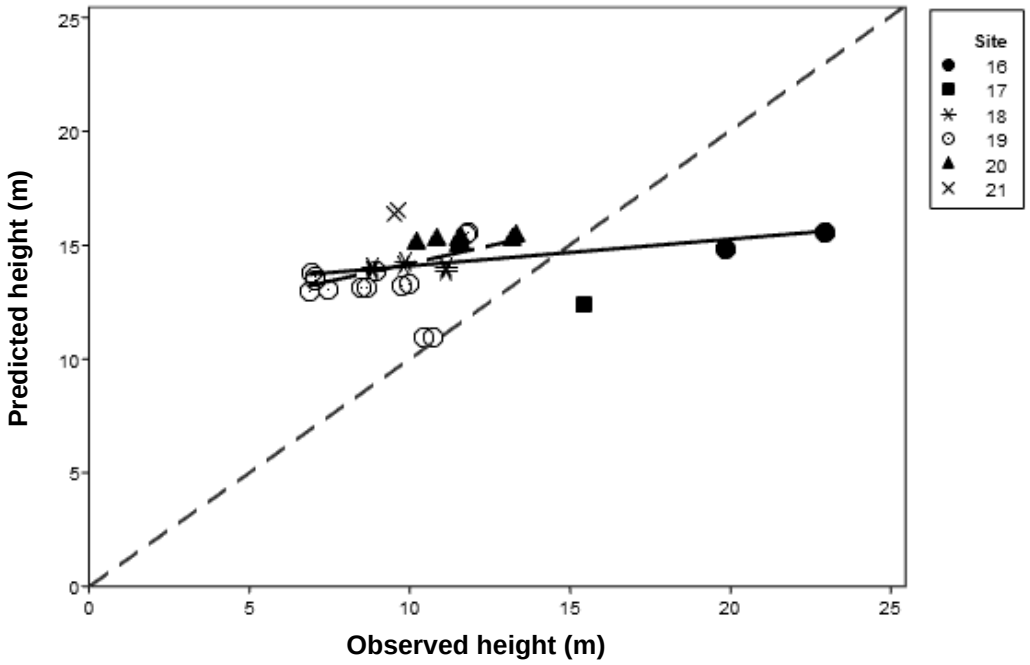


Figure 3.18. Relationship between mean observed and predicted height (m) for the six validation sites (R^2 = 0.06, RMSE 4.7 m). The solid black line represents the regression line (—). The dashed line represents the one-to one line (- - -), and the solid dashed black line represents the regression with Sites 16 and Site 17 removed (R^2 = 0.14, RMSE = 4.6 m).

The model provided a good fit to the observed mean stand density data across all validation sites (R^2 = 0.97, RMSE = 243 stems ha^{-1}) (Figure 3.19). The mean stand density of one plot from Site 19 was over-estimated by 69% (Figure 3.19). Overall, the model over-estimated mean stand density by 3%, therefore it provided a good fit to the validation dataset across all sites (Figure 3.19).

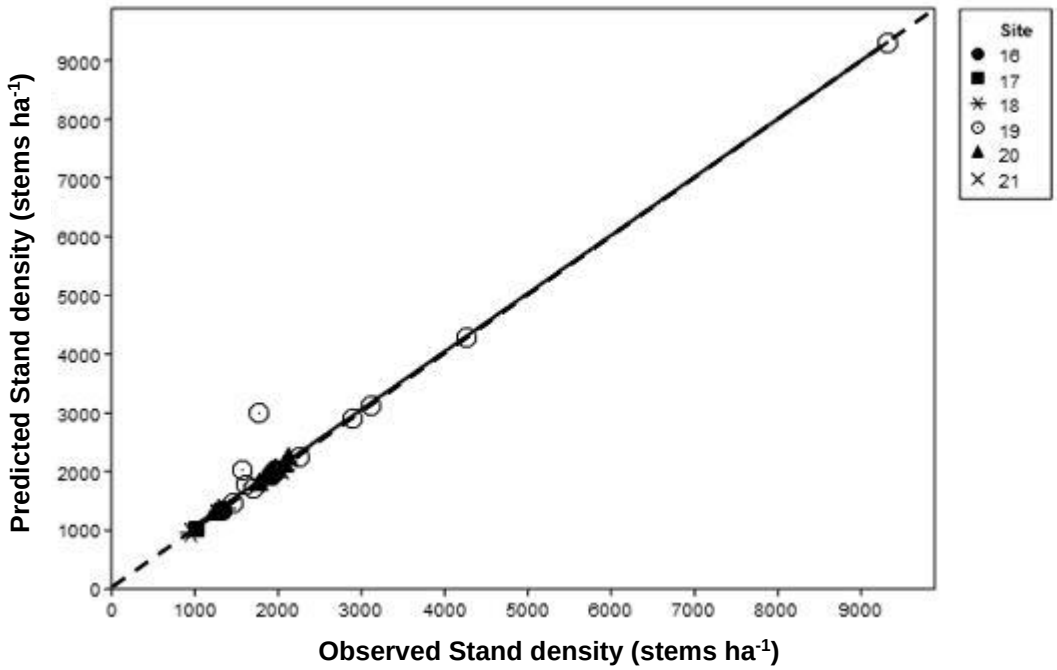


Figure 3.19. Relationship between mean observed and predicted stand density (stems ha^{-1}) for the six validation sites. The solid black line represents the regression line (—) (R^2 = 0.97, RMSE = 231 stems ha^{-1}). The dashed line represents the one-to one line (- - -), and the solid dashed black line represents the regression with Sites 16 and Site 17 removed (R^2 = 0.97, RMSE = 243 stems ha^{-1}).

The predictions of the 3-PG model for the validation sites were of variable accuracy. Mean stand density was the most accurately predicted variable, followed by mean stem diameter (Figure 3.15 & Figure 3.19). The model over-estimated mean diameter, mean basal area, mean volume and mean height across the slightly younger validation sites where mean stem diameters were smaller (Figure 3.15, Figure 3.16, Figure 17 & Figure 3.18). In addition to this, mean stem diameter, mean height, mean basal area and mean volume were under-estimated by the model at sites with larger mean stem diameters (Figure 3.15, Figure 3.16, Figure 3.17 & Figure 3.18).

Overall, the 3-PG model over-estimated mean stem diameter, mean basal area, mean volume and mean height at sites with smaller mean stem diameters for both the calibration and validation dataset. The model under-estimated tree size at sites with larger mean stem diameters. The model provided a good fit to the observed mean stand density data across both calibration and validation sites, with an $R^2 \geq 0.76$ and low RMSE $\leq$ 594 stems ha^{-1} (Figure 3.14 & Figure 3.19).

3.5 Discussion

Despite the over-predictions of growth across most calibration sites, the results from this study indicate the 3-PG model was able to predict mean stem diameter, height and stand density of tōtara in the calibration dataset with a reasonable amount of accuracy and small error ($R^2 \geq 0.60$). However, the model was not able to predict mean basal area and volume for the calibration dataset, as predictions were less accurate with more error ($R^2 \leq 0.50$). The overall performance of the model did not improve when the model was tested using the validation dataset. The model provided a good fit to the observed mean stand density across all validation sites $R^2 \geq 0.97$ (Figure 3.19). The results of this study identified the ability of 3-PG to simulate the effects of site and climate on productivity of tōtara across a range of sites. The model did not provide highly reliable predictions of tree growth across all calibration and validation sites and there were large variations in both datasets which were unable to be explained by the model. Some of this variation is likely to be due to the range of site ages (10 – 120 years) and the variation in physical characteristics and growth rates of sites included in the datasets which is expected when modelling both planted and naturally regenerated forest stands (Landsberg *et al.*, 2003). The 3-PG model generally over-estimates growth for stands with low stand density and large stem diameters (Landsberg *et al.*, 2003). However, the model unexpectedly over-estimated mean basal area and mean volume for sites with small mean stem diameters and small basal area from both the calibration and validation datasets. This could potentially be due to issues within the model or because of the limited amount of reliable data for model calibration and validation for these variables.

An area of interest to investigate further would be the model's predictions of basal area. The model was able to predict mean stem diameter and mean stand density across all sites for the calibration dataset with a reasonable amount of accuracy but, it is unknown why the model was unable to provide a good fit to observed mean basal area, as it is a function of these two growth variables. An earlier study by Meason *et al.* (2017) found similar over-estimates between the observed and predicted mean basal area data when modelling the productivity of Douglas-fir in New Zealand. As the issues with mean basal area are similar even though different species were modelled, it is likely this is probably a weakness of the model and not with the parameter values. However, further research is needed to clarify what part

of the model is causing the over-estimates and how it can be resolved (Meason *et al.*, 2017). This process was beyond the scope of the project.

The 3-PG model provided reasonably good predictions of growth for the calibration dataset, with the model predicting growth at younger sites more successfully than the older sites. This is more than likely due to the lack of data for these sites compared to the age and size of the stands. For example, Site 8 and Site 15 are both planted sites ≤ 30 years old and have ≥ four mensuration records for their age. These records include the initial stand density and plant date, mortality rates over time and the regular collection of mensuration data. This can be compared to the other calibration sites which were older and had substantially less information available. All of the other sites in the calibration and validation datasets were ≥ 60 years old, with most sites only having two previous mensuration records to provide information on the growth which has occurred over decades (Table 3.1 & Table 3.2). As such, the site history information was estimated from general knowledge of naturally regenerated stands and previous site information during the initial model calibration stage. For example, if the initial stand density of a naturally regenerated site was not known, it was assumed the site had an initial stand density of 6000 stems ha^{-1} because naturally regenerated tōtara can have very high stand densities (Bergin, 2001). As the stand density index (SDI) developed in Chapter 2 was not available during the time of modelling, natural self-thinning events within stands were estimated by assuming the events took place between the initial establishment date and the recorded mensuration periods. The reduction in stand density from these events and the age at which they occurred were estimated to improve the fit of the model to the observed growth data. Overall, a more robust dataset is required with known site history data for the model to provide better estimates of growth when compared to observed data.

For the validation dataset the poor performance of the model against the growth variables of mean stem diameter, mean basal area, mean height and mean volume is likely due to the lack of site data and silvicultural history. The six validation sites also had no soil physical or chemical data available compared to the calibration sites. Four of these sites (Sites 18-21) were used in a previous study where some mensuration and site history records were recorded, but the details around the site, size of plots and stand density of these naturally regenerated sites were poor

(Bergin, 2001). The remaining two validation sites included one planted site and one naturally regenerated site (Site 16 and Site 17). Both sites had less plots and site history data compared to the other validation sites. Site 16 and Site 17 were deemed outliers in the validation dataset as they had large stem diameters and were consistently under-estimated by the model compared to the other validation sites. The removal of these sites only slightly improved the fit of the regression for stem diameter (Figure 3.15). The model was able to predict mean stand density accurately for the validation sites with an $R^2 \geq 0.97$ and a low RMSE possibly because density is a strong and predictable function of age and it is likely the estimations based on general knowledge of self-thinning were reasonably accurate. For the other variables the validation dataset is likely to be of too narrow range, resulting in a lower overall $R^2 \leq 0.25$. It is important when evaluating growth models that a sufficient size and range of data is used to accurately calibrate and test the performance of the model, or else it could be costly if management regimes for forests were based on this data (Vanclay & Skovsgaard, 1997; Spittlehouse & Stewart, 2004). Therefore, in future studies the validation dataset should include a larger number and wider range (age, stand density, growth rates) of sites over which the model is validated against to accurately test the performance of the model.

Overall, the hypothesis was not supported by the results as the 3-PG model did provide a good fit to stem diameter, height and stand density for the calibration dataset with an $R^2 \geq 0.60$ and a low RMSE error, but it was unable to accurately predict basal area and volume. The performance of the validation dataset was poor with an $R^2 \leq 0.25$ and a high RMSE error for four of the growth variables. However, the model provided a good fit to mean stand density with an $R^2 \geq 0.95$ and a low RMSE error. These results suggest that predictions from the calibration dataset for mean stem diameter, mean height and mean stand density are useful as they can provide a basis for further research to continue to improve the model. The model was able to provide estimates of growth for tōtara even with a very small calibration dataset, which suggests this model could be appropriate to use for predicting biomass and yield estimates for the species once it has been further calibrated and validated. Therefore, there is potential for landowners or forest managers to use this model to predict yields of tōtara with the knowledge that the model requires further calibration for greater accuracy. This information could then be compared against a tōtara stand near the suggested site to ensure the predictions from the model are

realistic and could be used to inform management decisions (e.g. initial stocking and/or thinning).

3.5.1 Limitations

One of the main constraints to this study was the limited site history data and lack of soil physical and chemistry data for the calibration and validation of the sites. It is recommended that research across a wider range of sites and soil types is conducted to increase the quality and quantity of data available for growth modelling. As tōtara trees have not been well studied, model parameters for this species were not readily available. These parameters were obtained from literature, calculated from the collected calibration dataset, or left as default values that are based on other species. Further studies can probably achieve better results if they focus on directly measuring these parameter values. For example, specific leaf area (SLA) values were increased from the literature value for tōtara as the model was under-estimating leaf area index across all plots. Collecting foliage samples from a random number of trees across sites should enable a more accurate canopy leaf area index to be calculated for the model. Alternatively, if the measured SLA is confirmed to be lower than the value fitted during model calibration, this would indicate that changes are needed in parameters related to the proportion of biomass allocated to foliage (Landsberg *et al.*, 2003).

The data from the VSCN provided a consistent source of climate data for the 3-PG model. However, as this climate data was only available from 1972 and the majority of tōtara trees in this study were older than 47 years old, this climate data was replicated to provide climate data for trees that were older than the available climate dataset. Therefore, this data would not have accounted for any major climatic events (e.g. drought or floods) which may have influenced the growth of the species. For future studies, it is recommended site and soil monitoring is conducted using soil moisture, light and temperature loggers. This could identify local site variations which the VSCN data and fundamental soil layer maps from Landcare Research may not have accounted for due to the larger spatial scale of the data.

Although process-based models like 3-PG can work with a limited dataset, increasing the sample size of the study to include more calibration sites in theory

should help improve the fit and accuracy of calibration (Landsberg *et al.*, 2003). The calibration dataset used to estimate parameter values was quite small and was potentially less reliable than that of a larger dataset. Furthermore, any inaccurate parameter estimates are likely to have a larger effect on the results, particularly for parameters that are more important in the model. Therefore, it is recommended a sensitivity analysis is used in future studies to identify which parameters are more important for growth and should be the focus of further data collection to improve the overall reliability of the model (Landsberg *et al.*, 2001; Landsberg *et al.*, 2003; Esprey *et al.*, 2004). Future studies should ideally use sites with reliable information regarding stand age, initial stand density, when and what type of silvicultural treatments occurred, and at least three mensuration datasets. Much of this information is not available for sites with naturally regenerated tōtara trees, but there are methods of improving these datasets, such as analysing wood cores to age trees and developing a stand density index to help predict thinning events over time for tōtara (Reineke, 1933; Bergin & Kimberley, 2012). Ideally, most studies would not include naturally regenerated stands in the models, but since a large part of the potential timber and carbon industry involves these stands it is important to find ways to improve the quality of the data rather than removing these sites.

An important component for growth of any species is the fertility of the site (Landsberg *et al.*, 2003). As there is currently no soil fertility index available which we can use to interpolate the soil test results analysed from the calibration dataset in Chapter 2, we were unable to use these results for modelling. Therefore, we assumed all sites were reasonably fertile by setting the fertility modifier to 0.6. After all of the other parameters in the model had been adjusted to provide the best fit for the calibration data, we assumed the differences in growth between the observed data and the predictions from the model were probably due to the level of fertility. The fertility rating of each site was adjusted to improve the fit to the observed growth data by increasing or decreasing the fertility ratings. We assumed sites which were growing in soils with low fertility (e.g. Site 9 and Site 11) had a lower fertility rating closer to 0.2 to 0.3 and for sites we assumed were growing in more fertile soils (e.g. Site 12 and Site 13) we increased the fertility rating to 0.7. The same adjustment process was used for the validation sites. For future research, it is recommended that more information regarding the soil fertility and productivity of each plot is collected to develop a soil fertility index which could be used to

standardise the fertility ratings and remove the potential bias of adjusting the individual fertility ratings to get the model to fit the observed data (Landsberg *et al.*, 2003; Meason *et al.*, 2017). A sensitivity analysis should be used to identify the level of influence fertility has on the model's predictions, or whether other parameters have more influence and need further fine tuning to provide reliable estimates for the growth of tōtara (Esprey *et al.*, 2004; Weiskittel *et al.*, 2011).

3.6 Conclusion

The 3-PG model was able to provide predictions of growth variables to a reasonable level of accuracy. However, the model was unable to explain a large portion of the variation in the validation dataset and tended to over-estimate tōtara growth at most sites. Even though the predictions may not be highly reliable, they are still better than attempting empirical predictions from a limited mensuration dataset, because there is simply not enough data for the traditional look-up tables used for better known species. This study underlined the importance of a combination of modelling and quality data collection (i.e. site history and soil information) to ensure a sufficient amount of data regarding the sites and species are available to inform forestry management. Further research should continue to increase the size of this dataset and further refine the 3-PG model.

3.7 Appendix B

Table 3.3. Soil Textural Information for the twenty-one study sites retrieved from Landcare Research's New Zealand Fundamental Soil Layer (FSL) textural classification map.

Site	Soil Texture
1	Clay
2	Clay
3	Clay
4	Clay
5	Clay
6	Clay Loam
7	Clay
8	Clay
9	Sandy Loam
10	Clay Loam
11	Sandy Loam
12	Clay Loam
13	Loamy Sand
14	Loam
15	Clay Loam
16	Clay
17	Clay Loam
18	Clay
19	Clay Loam
20	Clay
21	Clay

Table 3.4. The parameter names and values used to calibrate 3-PG for *Podocarpus tōtara*.

Biomass partitioning and turnover	Abbreviation	Tōtara
Allometric relationships & partitioning		
Foliage:stem partitioning ratio @ D=2 cm	pFS2	0.81
Foliage:stem partitioning ratio @ D=20 cm	pFS20	0.22
Constant in the stem mass v. diam. relationship	aS	0.0455
Power in the stem mass v. diam. relationship	nS	2.5243
Maximum fraction of NPP to roots	pRx	0.6
Minimum fraction of NPP to roots	pRn	0.25
Litterfall & root turnover		
Maximum litterfall rate	gammaFx	0.03
Litterfall rate at t = 0	gammaF0	0.001
Age at which litterfall rate has median value	tgammaF	36
Average monthly root turnover rate	gammaR	0.015
NPP & conductance modifiers		
Temperature modifier (fT)		
Minimum temperature for growth	Tmin	5
Optimum temperature for growth	Topt	27
Maximum temperature for growth	Tmax	35
Frost modifier (fFRost)		
Days production lost per frost day	kF	3
Soil water modifier (fSW)		
Moisture ratio deficit for $f_q = 0.5$	SWconst	0.55
Power of moisture ratio deficit	SWpower	6
Atmospheric CO2 modifier (fCO2)		
Assimialtion enhancement factor at 700 ppm	fCalpha700	1.4
Canopy conductance enhancement factor at 700 ppm	fCg700	0.7
Fertitlity effects		
Value of 'm' when FR = 0	m0	0
Value of 'fNutr' when FR = 0	fN0	0.6
Power of (1-FR) in 'fNutr'	fNn	1
Age modifier (fAge)		
Maximum stand age used in age modifier	MaxAge	400
Power of relative age in function for fAge	nAge	4
Relative age to give fAge = 0.5	rAge	0.95
Stem mortality & self-thinning		
Mortality rate for large t	gammaNx	0
Seedling mortality rate (t = 0)	gammaN0	0
Age at which mortality rate has median value	tgammaN	0
Shape of mortality response	ngammaN	1
Max. stem mass per tree @ 1000 trees/hectare	wSx1000	900
Power in self-thinning rule	thinPower	1.2
Fraction mean single-tree foliage biomass lost per dead tree	mF	0
Fraction mean single-tree root biomass lost per dead tree	mR	0.2
Fraction mean single-tree stem biomass lost per dead tree	mS	0.2
Canopy structure and processes		
Specific leaf area		
Specific leaf area at age 0	SLA0	20
Specific leaf area for mature leaves	SLA1	18

Biomass partitioning and turnover	Abbreviation	Tōtara
Age at which specific leaf area = (SLA0+SLA1)/2	tSLA	2
Light interception		
Extinction coefficient for absorption of PAR by canopy	k	0.5
Age at canopy cover	fullCanAge	15
Maximum proportion of rainfall evaporated from canopy	MaxIntcptn	0.15
LAI for maximum rainfall interception	LAImaxIntcptn	5
Production and respiration		
Canopy quantum efficiency	alpha	0.06
Ratio NPP/GPP	Y	0.47
Conductance		
Minimum canopy conductance	MinCond	0
Maximum canopy conductance	MaxCond	0.02
LAI for maximum canopy conductance	LAIgcx	3.33
Defines stomatal response to VPD	CoeffCond	0.05
Canopy boundary layer conductance	BLcond	0.2
Wood and stand properties		
Branch and bark fraction (fracBB)		
Branch and bark fraction at age 0	fracBB0	0.5
Branch and bark fraction for mature stands	fracBB1	0.1
Age at which fracBB = (fracBB0+fracBB1)/2	tBB	5
Basic Density		
Minimum basic density - for young trees	rhoMin	0.48
Maximum basic density - for older trees	rhoMax	0.48
Age at which rho = (rhoMin+rhoMax)/2	tRho	4
Stem height		
Constant in the stem height relationship	aH	1.4093
Power of DBH in the stem height relationship	nHB	0.7345
Power of stocking in the stem height relationship	nHN	0
Stem volume		
Constant in the stem volume relationship	aV	0.9796
Power of DBH in the stem volume relationship	nVB	1.859
Power of stocking in the stem volume relationship	nVN	0
Conversion factors		
Intercept of net v. solar radiation relationship	Qa	-90
Slope of net v. solar radiation relationship	Qb	0.8
Molecular weight of dry matter	gDM_mol	24
Conversion of solar radiation to PAR	molPAR_MJ	2.3

Chapter 4

Discussion

4.1 Introduction

The overall objectives of this thesis were to quantify growth, investigate site productivity drivers for tōtara across sites, and model this growth with 3-PG. This chapter summarises the main site productivity drivers investigated in Chapter 2 and discusses how these results could potentially be used to inform future management of the species. In addition, this section highlights the key findings from Chapter 3 regarding the performance of the 3-PG growth model at predicting growth of tōtara across both calibration and validation sites. This chapter concludes with recommendations for future research which may provide relevant information to help landowners, forest managers and other organisations fulfil their objectives regarding tōtara.

4.1.1 Key site productivity variables

Multiple climatic and edaphic factors were identified as important drivers which influence productivity of tōtara. The multiple linear regression analysis examined 22 site productivity variables and selected 11 variables that were significantly related to productivity ($R^2 = 0.95$, $C(p) = 5.09$). Temperature (mean, maximum and minimum), rainfall and elevation were selected as the main climatic drivers. Mean annual temperature was positively correlated with productivity. This may explain why regenerating tōtara trees are more abundant in northern and lowland regions of the North Island where mean annual temperatures are higher than other parts of the country (Hinds & Reid, 1957; Bergin, 2001, 2003a). Maximum and minimum annual temperatures were both selected as significant factors relating to productivity ($p \leq 0.001$) and had a negative correlation with productivity. This finding suggests that productivity decreases as maximum and minimum temperatures increase. Earlier studies have corroborated this reduction in productivity for maximum annual temperatures in glasshouse and nursery studies (Hawkins & Sweet, 1989a). Higher maximum annual temperatures may reduce rainfall which could offset the ability of the species to survive in conditions which are too far above their optimal mean temperatures. This could be due to the species

lack of tolerance for long duration and/or intense drought conditions (Wardle, 1985; Hawkins, 1988; Bergin, 2003a; Simpson, 2017).

Interestingly, the negative correlation with minimum temperature suggests that as minimum annual temperatures increase (i.e. warmer temperatures), productivity decreases. It is currently unclear why this result has occurred, as previous studies have identified productivity typically decreases in response to lower minimum annual temperatures (Beveridge, 1962; Hawkins *et al.*, 1991; Bergin, 2003a; Simpson, 2017). Therefore, it is recommended further research should investigate this relationship to identify whether collinearity between the three temperature measures in the multiple linear regression analysis may have influenced this correlation, or whether the slightly warmer minimum temperatures at these sites could have possibly reduced water availability for growth. Additionally, as the majority of sites investigated were in Northland and the Waikato region, this correlation could have been influenced by the small range of minimum temperatures (0.5 to 7°C). Furthermore, future studies could widen the range of sites investigated to incorporate sites where minimum annual temperatures are lower (e.g. higher frequency of frosts) to explore this relationship with temperature further.

Rainfall was also identified as a significant driver of productivity. The negative correlation with rainfall suggests productivity decreases as rainfall increases. This could be related to the soil physical properties across sites. As the sites investigated in this study had a limited range of rainfall (1013 to 2288 mm), these sites could be growing on soils that have a higher soil water holding capacity and lower porosity, which could lead to waterlogged soils if mean annual total rainfall increases. This could explain why productivity decreases, due to the species intolerance of waterlogged soils (Bergin, 2000; Simpson, 2017). However, this negative correlation between rainfall and productivity is likely to differ across soil types and regions. For example, tōtara growing in Canterbury are typically found on alluvial floodplains as mean annual total rainfall in the region is low (McSweeney, 1982; Simpson, 2017). Therefore, if mean annual total rainfall increases, the productivity of tōtara could increase as the trees may benefit from the additional rainfall, as the soil physical properties of alluvial floodplains typically have lower soil water holding potential and higher porosity which can prevent the soils from waterlogging. Further research is recommended to investigate this relationship across tōtara sites

in the North and South Island to identify how productivity differs in response to higher and/or lower mean annual total rainfall across different soil types and regions.

Elevation was also found to be significantly related to productivity in the multiple linear regression analysis. This finding was similar to an earlier study by Dowling and Steward (2018) that investigated tōtara productivity across Northland using non-parametric empirical growth models. Their study found that productivity tended to be higher at sites that were located at elevations greater than 160 m above sea level (asl). However, their study concluded that elevation was likely to be a proxy for other factors such as soil type and land use which were likely to be the main drivers of high site productivity (Dowling & Steward, 2018). Additionally, their study found latitude was a poor predictor of productivity which was supported by the multiple linear regression analysis in our study that removed latitude from the final model. Overall, these findings suggest that elevation can be used as a proxy for temperature, as the two variables are correlated. However, further research is recommended to investigate and quantify the other significant climatic and edaphic factors to identify the main drivers of site productivity. This information could help improve the management of current tōtara stands and could identify sites which are more suitable for higher productivity.

Soil physiochemical properties were also significantly related to the productivity of tōtara across sites. Soil concentrations of total phosphorus, magnesium, potassium, calcium and manganese were selected as important drivers of productivity in the multiple linear regression. In previous radiata pine plantation studies, these soil nutrients have been identified as key nutrients that prevent deficiencies which can reduce productivity (Mead & Gadgil, 1978; Turner & Lambert, 1986; Watt *et al.*, 2008; Davis *et al.*, 2015). As the concentrations of these soil nutrients required for growth of tōtara have not been documented. Further research could investigate how the concentrations of these soil nutrients vary by soil type and land use under naturally regenerated and planted tōtara stands. This information could be used to identify nutritional problems that reduce productivity across sites. This would benefit landowners and forest managers as they could incorporate the application of these soil macro and micronutrients into fertiliser regimes to ensure sufficient concentrations of these nutrients are available to maximise productivity.

The role of available soil phosphorus as a growth limiting nutrient in forest systems has been well documented in the literature (Baylis, 1969; Hawkins & Sweet, 1989b; Watt *et al.*, 2008; Jansa *et al.*, 2011; Davis *et al.*, 2015). Previous studies have identified the importance of symbiosis between root mycorrhizal species that aid plant uptake of mineral nutrients, particularly phosphorus (Baylis, 1969; Brundrett & Abbott, 2002; Siddiqui & Pichtel, 2008; Dickie & Holdaway, 2011; Davis *et al.*, 2015; Waring, 2017). However, there has been no consensus in the literature about the type of mycorrhizae present on tōtara and the concentrations of nutrients these associations may provide to support or improve productivity (Baylis, 1969; Hawkins & Sweet, 1989b). Therefore, it would be interesting to investigate the types of mycorrhizae present in naturally regenerated stands and to compare the results with those grown in planted stands to identify any differences in nutrient uptake and growth. The soil phosphorus levels (50 to 300 mg^{-1} kg^{-1}) across calibration sites were potentially sufficient for uptake and growth as they are within the targeted concentration range for phosphorus required for growth in radiata pine plantation forests (Watt *et al.*, 2005; Watt *et al.*, 2008; Hill & Sparling, 2009). Earlier experimental studies by Hawkins and Sweet (1989b) identified tōtara seedlings responded positively to soil phosphorus. However, the level of phosphorus fertility required for growth of tōtara has not been documented (Hawkins & Sweet, 1989b; Bergin, 2000, 2003a). A point of interest to investigate further would be to identify the concentration of soil phosphorus required to ensure tōtara productivity is not limited by this soil nutrient. This could be achieved by developing a soil fertility index by increasing the number of sites in the study to investigate a wider range of soil types and sites of different total and available phosphorus concentrations. Further, if sites are found to have low soil phosphorus it would be interesting to investigate the response of tōtara to fertiliser, to see if the range of potential growing sites for tōtara could be extended by fertiliser application, as previous studies have found with radiata pine (Mead & Gadgil, 1978; Smith *et al.*, 2000; Davis *et al.*, 2015).

In contrast to phosphorus, soil nitrogen was not found to be significantly related to productivity, but the level of soil nitrogen across both planted and naturally regenerated sites was typical of radiata pine plantation forests (0.2% to 0.7%) (Watt *et al.*, 2008; Davis *et al.*, 2015). This finding suggests that soil nitrogen may not be a limiting nutrient at the study sites which may be a result of previous agricultural

practices (e.g. fertiliser treatment). Future research could focus on investigating the differences between the soil chemical properties *in-situ* and *ex-situ* of the tōtara stands to identify if site history is linked to the soil nitrogen levels and how this affects the productivity of tōtara (Williams *et al.*, 2011).

Soil physical properties were also selected as significant drivers of productivity. As the sites used in this study are known to not to have high soil salinity, the differences in apparent electromagnetic conductivity (EC_a) across sites were considered to be due to soil textural properties and soil water holding capacity (Sudduth *et al.*, 2003; Grisso *et al.*, 2005; Jiang *et al.*, 2007; Zhu *et al.*, 2010; Gallart *et al.*, 2019). Both HCP (horizontal) and PRP (perpendicular) measure EC_a of the soil from the same instrument, however, they measure it at different depths of exploration with PRP measuring to a depth of 0.5 m and HCP measuring to a depth of 1.5 m (Doolittle & Brevik, 2014; Dualem Inc, 2014). They also have different sized measurement fields as there is a 1.1 m separation between the transmitter and PRP receiver and a 1 m separation between the transmitter and the HCP receiver (Grisso *et al.*, 2005; Doolittle & Brevik, 2014). The findings from the multiple linear regression analysis in Chapter 2 suggest that the soil physical properties at greater depths measured by the HCP receiver may be more important for productivity than shallow soil physical properties measured by the PRP receiver. Low EC_a values ($\leq$ 60 mS m^{-1}) are associated with coarser-textured soils such as sand and silt (Grisso *et al.*, 2005; Gallart *et al.*, 2019). These soils have higher soil porosity and lower soil water holding capacity, compared to finer-textured soils (e.g. clay) (Grisso *et al.*, 2005; Gallart *et al.*, 2019). High EC_a values (> 60 mS m^{-1}) are associated with finer-textured soils (Grisso *et al.*, 2005; Gallart *et al.*, 2019). The majority of tōtara sites investigated in Chapter 2, had high HCP EC_a values, which suggests that these sites are associated with finer-textured soils such as clay at depths between 0.5 m and 1.5 m. This could explain why tōtara prefer to grow in these soil types as soil water holding capacity is higher and soil porosity is lower. Additionally, two of the lowest productivity sites were associated with the lowest EC_a values which suggests that the sand or silt textural properties may not be suited to tōtara. This could be due to the lower soil water holding capacity and higher soil porosity of these soil types. However, productivity at these sites is likely to be influenced by other environmental factors such as temperature, rainfall and competition, which could contribute to the overall productivity of these stands.

Further research is recommended to investigate a wider range of sites, across a broader range of soil types to identify whether the depth of bedrock, organic matter, effective rooting depth, soil moisture and topography may have influenced the high EC_a values (Grisso *et al.*, 2005). Additionally, investigating the soil profile down to a depth of 1.5 m may provide more information on soil water holding potential, nutrient availability and porosity of the surface and deeper soil layers. This information could be used in future studies to develop a local site map of EC_a values to identify areas where the soil physical properties may be more suitable for tōtara. Furthermore, the importance of HCP and PRP did vary by the type of multiple linear regression. This could be due to the high collinearity between variables which may have prevented PRP from being selected as a variable that was significantly related to productivity.

Rieneke's stand density index (SDI) approach provided a measure of the potential maximum and optimal stand densities for tōtara (Reineke, 1933; Drew & Flewelling, 1979; Long, 1985). Studies that have used SDI models similar to this, have found that they are valuable tools for forestry as they can translate management objectives to inform density management of forest stands (Long, 1985; Dash *et al.*, 2019). For example, if the objective is for timber, the trees could be planted at higher or lower stand densities depending on the desired timber yield for harvest (e.g. higher total volume per tree or higher timber yield per hectare). Previous studies on radiata pine plantations have identified that these differences could affect the economic returns for landowners (Dash *et al.*, 2019). To my knowledge, this is the first time an SDI model has been developed for tōtara. Therefore, this novel information could be used by landowners and forestry managers to identify the optimal and maximum stand densities for tōtara to maximise stand productivity and as a reference for future plantings (Drew & Flewelling, 1979; Long, 1985). The tōtara plots which were below the 35% self-thinning line are considered under-stocked. This means that although the trees are larger in size, the total yield of timber per hectare from the stand is likely to be lower compared to more densely stocked stands. Therefore, these stands may not be considered optimal as the site is not fully utilised (Drew & Flewelling, 1979). Alternatively, a benefit to these understocked stands is that the stands do not require rigorous silvicultural management which can be costly. Understocked stands could

be left to grow without management until the 55% relative density line where they are likely to require silvicultural management (e.g. thinning) to maintain productivity at larger stem sizes. In theory, the area between the 55% relative density line and 100% relative density line is referred to as the competition-induced mortality zone, where intra-specific competition is higher, and growth is slower between trees (Drew & Flewelling, 1977, 1979). Therefore, it may result in an increased tree mortality if the stands are not managed (Drew & Flewelling, 1979; Long, 1985). The maximum self-thinning line at 100% relative density fit the tōtara data well as no sites exceeded this potential maximum size-density relationship. This line indicates that stands close to this line are near the maximum size-density relationship that can exist for a given stand density and tree size. This suggests that tōtara stands could be managed around this line to maximise stand productivity, or depending on the age of the tree it could provide an indication for landowners that the stand is ready for harvest (Drew & Flewelling, 1979).

For the future establishment of planted stands or management of naturally regenerated tōtara stands, this SDI model could be used to inform the density of plantings, to maximise stand productivity without compromising the mean stem size of the trees. However, as the SDI model was developed from the small calibration dataset, it is important to validate this model with a wider range of sites to identify whether the model could potentially be used to inform management decisions specific for tōtara. Subsequently, if a size-density and age relationship could be identified from these findings, this research may help improve future growth modelling of the species by helping identify natural self-thinning events. Earlier studies have identified a site index for volume and age of tōtara, however, these indices have not factored in mortality (Bergin, 2000, 2001, 2003a). Furthermore, if a SDI model is developed for tōtara that can identify the age of mortality events, it could be used to inform what age/stand density silvicultural management such as thinning should be carried out to maximise growth. This could also be used to identify self-thinning events in naturally regenerated stands to identify how the productivity of tōtara stands respond to different periods of self-thinning.

The comparison of the four volume equations in Chapter 2 highlighted the improvements species-specific volume equations could provide for forest inventory measurements and growth modelling. The equation developed by Todoroki and

Steward (2019) provided more reliable volume estimates for tōtara than the equations from Ellis (1979), Beets *et al.* (2012) and Coomes *et al.* (2002). These equations were selected from previous studies which have relied on volume and allometric equations from other species such as rimu and kāuri, or combined data from multiple species (Bergin, 2001; Coomes *et al.*, 2002; Bergin & Kimberley, 2003; Richardson *et al.*, 2009; Beets *et al.*, 2012; Dowling & Steward, 2018; Steward *et al.*, 2018). As the majority of tree biomass is stored within the stem (Landsberg & Sands, 2011), equations which under-estimate or over-estimate volume can lead to miscalculations of merchantable stand volume and potentially a loss of economic returns (Xing *et al.*, 2019). Although the Todoroki and Steward (2019) equation provided a step forward towards predicting stem volume for tōtara more accurately, the equation has not yet been tested in other studies. Further research should focus on investigating the foliage and stem biomass for tōtara as there is very limited data available on these components from the literature. Subsequently, the carbon equation developed by Beets *et al.* (2012) was modified by adding the volume equation developed by Todoroki and Steward (2019) in an attempt to calculate carbon for the species. Future research could focus on developing an equation which can be used to calculate the volume and carbon sequestration rate for indigenous conifers for the NZ ETS carbon look-up tables.

Overall, multiple site factors can be used to predict site productivity of tōtara with a high R^2. Previous studies have identified that tōtara can grow across a wide range of climatic and environmental conditions, however, few of these studies have provided links to the key site productivity drivers and how they potentially influence growth across sites (Hinds & Reid, 1957; Hawkins, 1988; Bergin, 2001; Bergin & Kimberley, 2003; Kimberley *et al.*, 2014; Simpson, 2017). While tōtara can be grown across a wide range of regions and sites, this study found that there are multiple climatic and edaphic factors which could be used to predict site productivity of tōtara in planted and naturally regenerated stands. From these findings, we can speculate that productivity is likely to be higher in tōtara stands with warm mean annual temperatures and moderate annual rainfall. In terms of site fertility, phosphorus and the key macro and micronutrients which typically prevent deficiencies in forests are significant for productivity along with soil types that may have higher soil water holding capacity and lower porosity. Additionally, productivity is likely to be affected by intra-specific competition, therefore the SDI

model could also be used as a reference for landowners and forestry managers to inform silvicultural management to maximise productivity and improve economic returns. Further research should be conducted to provide improvements to the current quality of data available which could be used to inform management of these sites for timber or carbon forestry.

4.1.2 Growth model performance

The 3-PG forest growth model predicted the growth of tōtara across sites with variable success. The 3-PG model performed moderately well with predicting stem diameter, height and stand density from the calibration dataset, however, it was unable to accurately predict basal area and volume which are the desired growth variables required to inform forestry management (Landsberg & Sands, 2011; West, 2014). Previous studies have identified that the 3-PG model generally over-estimates growth for stands with low stand density (Landsberg *et al.*, 2003). This may explain why the basal area was consistently over-estimated for the calibration sites with small stem diameters. Validation of the model against the independent dataset did not provide reliable estimates for growth as it over-estimated the majority of key growth variables. This could be due to a number of different factors and further investigation into the model's parameters and algorithms are recommended. This may provide more details as to whether the source of error is within the model, or with the quality of the data.

To my knowledge, this is the first time the 3-PG model has been parameterised and calibrated to predict the growth of tōtara across sites. Therefore, even though the results were not accurate, they indicate that process-based models like 3-PG could be used to model species with limited datasets to identify base line information on the growth over time and identify where additional research efforts should be directed to improve predictions. This can be compared to the traditional empirical models which require substantially more information before they can be implemented. Further research is recommended to identify whether increasing the size and quality of the dataset to include a higher number of sites and information on site history could potentially improve the performance of the model, or whether the parameters for tōtara may need to be revised. For example, foliage samples could be collected to investigate the SLA value for tōtara. If this value is confirmed

to be lower than the value fitted during model calibration, this would indicate that changes are needed in parameters related to the proportion of biomass allocated to foliage. Subsequently, an SDI index could be used which may help fill knowledge gaps regarding mortality events and key growth periods where competition may have influenced growth.

It is recommended that future studies continue to evaluate the model and test growth predictions against measured growth data across a wide range of sites, stand densities and tree ages to improve predictions of growth for tōtara. This information could potentially be helpful to identify when stands may be ready for harvest and to inform forest management which aims to increase the productivity of the stands through thinning regimes or fertiliser use. Further research could also use this model to project growth and productivity with different climate scenarios, or to produce maps which may be able to show the potential productivity of the species across regions of the North Island. This could help landowners, forest managers and other organisations identify the potential productivity of their land and whether planting tōtara would be a suitable option.

4.1.3 Limitations

One of the main limitations identified in this study was the small size of the tōtara dataset and the lack of quality data, including detailed site histories, stand histories (including management and stand density over time) and soil information, particularly for the validation sites. This information could provide more reliable estimates of growth and yield from the 3-PG model. Therefore, it is recommended that for future studies data collection should include growth mensuration data (e.g. stem diameter, height, stand density) in addition to foliage and soil sampling (physical and chemical properties). This could help refine parameters and identify a suitable soil fertility index which may prove useful to forest management and growth modelling. If new sites are included, wood core samples from trees should be collected to provide age information (Bergin & Kimberley, 2012).

The virtual climate station network (VCSN) provided a consistent source of monthly climate data for growth modelling. However, as data was not available prior to 1972, the climate data from the past 47 years was replicated to provide data

for trees that were older than the available climate dataset. Due to this, any major climatic events that may have reduced growth prior to 1972 are unaccounted for (e.g. drought events). Additionally, as the data is spatially interpolated across New Zealand daily on a 5 km grid, the large spatial scale of the data may not capture local site variations (e.g. solar radiation, rainfall, soil moisture and humidity) which may influence the productivity of these sites. For future research, it is recommended the VCSN data continues to be used as it currently provides the most reliable source of site specific climate data. However, in future studies it is recommended that long-term monitoring at sites is conducted as it may improve estimates of soil moisture, temperature, rainfall and solar radiation which could be used to adjust the model more specifically for each site. In addition to this, long-term monitoring of soil physical and chemical properties could also help identify any seasonal changes which could be important for growth, as the measurements were only taken at one point in time. The soil textures obtained from the fundamental soil layer maps may also not have provided a good representation of soil textural properties at forestry sites.

The multiple linear regression analysis using the backward elimination method, provided a good indication of the main climatic and edaphic variables influencing productivity of tōtara across the study sites. However, collinearity between variables could have influenced the multiple regression analysis and potentially prevented highly correlated variables (e.g. PRP and HCP) from being selected as significant drivers of productivity (Freund *et al.*, 2006; Der & Everitt, 2008). Additionally, as the method does not identify the individual R^2 values for the variables retained in the model, it is not known what variables contributed the most to productivity (e.g. mean temperature, rainfall or total phosphorus). For future studies, it is recommended that the multiple regression analysis is tested with an independent dataset to identify whether the same variables are selected, or whether another method could be used in conjunction with the backward elimination method to identify which of the significant variables selected in the multiple linear regression contributed the most to productivity (e.g. mean annual temperature or site fertility).

Throughout this study, all measured data and the data obtained for validation were assumed to come from one species (i.e. *Podocarpus tōtara*). We did not investigate

whether some of these trees may have been the specie's close relative (i.e. *Podocarpus laetus*). Further research could collect leaf samples for DNA tests to identify the species from the sites used in this study and when investigating new tōtara sites (Marshall *et al.*, 2015). It could be interesting to extend the scope of this study to include the two species and compare the productivity of Hall's tōtara with lowland tōtara across New Zealand, as it is currently not known how the productivity of the two species compares in planted and naturally regenerated stands. This information could identify that some genotypes or seedlings within each species may perform better in some regions than others.

4.1.4 Future recommendations

For future studies, it is recommended that each tōtara stand should be remeasured regularly every five years. Long-term monitoring of these sites could reduce the number of assumptions which were required for growth modelling and understanding the effects of natural self-thinning within the stands. It would be beneficial for site-specific monitoring using temperature and soil moisture loggers to examine the microclimates these trees grow in. This could help clarify the number of frost days experienced and provide more accurate estimates of available soil water. In addition, future research should continue to include a wider range of planted and naturally regenerated growing sites across more regions of New Zealand which will improve the current 3-PG growth model. It would be interesting to attempt to model other indigenous conifer species and see how the model performs. If the model provides reliable information for these species, a climate modelling study for these indigenous species could also be undertaken.

As tōtara is a long-lived species which grows at a slower rate than exotic pines and eucalypts, it is important that the use of the species is reserved for long-term management as landowners and forest managers are not likely to receive economic returns from plantings until the species are older. As the quantity of naturally regenerated tōtara is extensive in Northland, people's interest in developing sustainable harvest and milling operations within the region may increase alongside the demand for these services. This will likely lead to employment opportunities and financial benefits for the region. Furthermore, the species will provide ecological and cultural benefits such as erosion control, aesthetic value, habitat for

native birds and other animals, as well as allowing historic buildings to be repaired with the appropriate type of timber. The results from this thesis will provide further incentives to utilise indigenous forest species like tōtara as a resource for commercial and non-commercial forestry. Furthermore, it will be useful to landowners, forest managers and other organisations to quantify the commercial potential of tōtara stands for timber and carbon forestry.

4.2 Conclusions

In conclusion, multiple climatic and soil physiochemical properties were found to be important drivers of productivity in both planted and naturally regenerated tōtara stands. This information can be used as a basis to identify locations across the North Island that are most suited for planting tōtara or managing stands for timber or carbon forestry. The results from this study provide evidence that tōtara specific equations and the SDI index will improve current estimates of merchantable tōtara stands and inform density management, which will improve estimates of economic returns. In addition, this study found that the 3-PG growth model did not provide reliable estimates for all growth variables. However, it provided a basis for predicting growth of the species, which was not possible using traditional empirical models and current available datasets. The findings from this thesis highlights the importance of further research to provide regular growth data and long-term monitoring of tōtara sites to improve the quality of the data available for growth modelling and forest management. Overall, this research has improved the knowledge base available for tōtara and will help landowners, forest managers, iwi and the government grow and manage tōtara for both commercial and non-commercial purposes.

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